Fishery-impacted bottlenose dolphins of north-western Australia: Bycatch patterns, genetic status and abundance.

by

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Thesis publications

1. Allen SJ, Tyne J, Kobryn HT, Bejder L, Pollock KH and Loneragan NR (2014) Patterns of dolphin bycatch in a north-western Australian trawl fishery. PLoS ONE 9: e93178 doi:10.1371/journal.pone.0093178 (Chapter 2)

2. Allen SJ, Bryant K, Kraus RHS, Loneragan NR, Kopps AM, Brown A, Gerber L, Krützen M (in review) Genetic isolation between coastal and fishery-impacted offshore bottlenose dolphin (*Tursiops* spp.) populations of north-western Australia. Mol Ecol (Chapter 3)

3. Allen SJ, Loneragan NR, Bouchet P, Smith J, Nicholson K, McElligott DB, Kobryn HT, Pollock KH (in prep) Conservation implications of the abundance and fidelity of bottlenose dolphins (*Tursiops truncatus*) in a demersal trawl fishery. Scientific Reports (Chapter 4)

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Abstract

The incidental capture of cetaceans in fisheries threatens several species with extinction and represents a global conservation challenge. In order to assess the impacts of bycatch on dolphins in a north-western Australian trawl fishery, I (*i*) examined bycatch reported in skippers' logbooks and independent observer data; (*ii*) applied genetic methods to estimate dolphin population structure and connectivity; and (*iii*) conducted an aerial survey to estimate dolphin abundance across the fishery, simultaneously undertaking boat-based photo-identification to infer fidelity to the fishery. From 2003-2009, between 180 and 366 dolphins were caught across all management areas, depths and seasons. Independent observers reported more than double the dolphin bycatch reported in skippers' logbooks. Significant predictors of dolphin bycatch were fishing vessel, time-of-day and whether nets included Bycatch Reduction Devices (BRDs). Genetic evidence showed one panmictic population of trawler-associated common bottlenose dolphins (*Tursiops truncatus*), but isolation from all adjacent, coastal populations of Indo-Pacific bottlenose dolphins (*T. aduncus*). Abundance was estimated at 2,000-3,000 *T. truncatus* across 25,880 km^2. While the lack of correction factors for availability bias mean this is likely an underestimate, it is lower than previously thought. Trawler-associated individuals were photographically and genetically matched over periods of days to years. Recent skippers' logbook data suggest dolphin bycatch rates have increased since the BRDs were introduced. These results indicate that (*i*) only a considerable reduction in trawling effort is likely to reduce dolphin bycatch; (*ii*) the impacted population does not recruit from the adjacent coastal populations; and (*iii*) the number of dolphins interacting with trawlers is fewer than expected. The chronic bycatch of this protected species may affect the dolphin population's conservation status. As a consequence, the classification of acceptable limits of bycatch requires revision in light of these first estimates of the abundance and fidelity of bottlenose dolphins interacting with the Pilbara Trawl Fishery.

Declaration

I hereby declare that this work has not been submitted for a higher degree to any other university or institution and that, except where otherwise stated; this represents my own, original work.

Simon J. Allen

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Statement of the contributions to this Thesis

I was responsible for developing the overall directions, individual components, directing inputs from others, and writing first drafts and revisions of all drafts for the Thesis. My contributions and those of others for each chapter in the Thesis are summarised below.

Ch1: Introduction and objectives

Simon Allen: reviewed the literature; developed plan; wrote the introduction and objectives to this thesis.

Neil Loneragan: commented on structure and content of chapter; editorial input.

Ken Pollock: provided comments.

Ch2: Patterns of dolphin bycatch in a north-western Australian trawl fishery

Simon Allen: conceived and designed this chapter and element of the research, with Neil Loneragan, Lars Bejder and Ken Pollock; negotiated the acquisition of the data from the Dept. of Fisheries with Neil Loneragan; constructed tables; performed analyses and constructed figures with Julian Tyne and Halina Kobryn; wrote the chapter and the paper.

Julian Tyne, Halina Kobryn, Ken Pollock and Neil Loneragan: contributed to different elements of the various data analyses.

Neil Loneragan: commented on structure and content of the chapter.

All other co-authors: provided editorial input into the paper.

Ch3: Genetic isolation between coastal and offshore, fishery-impacted bottlenose dolphin (*Tursiops* spp.) populations of north-western Australia

Simon Allen: conceived this research question, with input from Michael Krützen; collected the vast majority of the data, with contributions from Michael Krützen and Alex Brown; constructed tables and figures with Michael Krützen and Halina Kobryn; wrote the chapter with editorial input from Kate Bryant, Michael Krützen, Anna Kopps and Neil Loneragan.

Kate Bryant, Anna Kopps and Livia Gerber: conducted the genetic lab work.

Robert Kraus and Michael Krützen: performed the advanced analyses of genetic data.

Ch4: Estimating the abundance and fidelity of bottlenose dolphins in the Pilbara Trawl Fishery

Simon Allen: conceived and designed this research, with support from Neil Loneragan, Amanda Hodgson and Ken Pollock; collected the data; constructed tables and figures, with Halina Kobryn; performed some analyses; wrote the chapter, with editorial input from Neil Loneragan, Phil Bouchet and Ken Pollock.

Joshua Smith: coordinated the aerial survey.

Phil Bouchet: conducted the distance sampling analyses.

Dee McElligott and Krista Nicholson: processed the photo-ID data.

Ken Pollock: advised on all statistical methods.

Neil Loneragan, Phil Bouchet and Ken Pollock: editorial input to writing the chapter.

Chapter Five: Conclusions and recommendations

Simon Allen: developed the plan and structure of the chapter through discussions with Neil Loneragan; wrote the synthesis, recommendations and conclusions.

Neil Loneragan: Discussions of plan, editorial input.

Chapter One: Introduction and objectives

1.0 Introduction

The incidental capture, or bycatch, of non-target species in fisheries presents an ongoing global conservation and fisheries management challenge (Hall et al. 2000; Read et al. 2006; FAO 2014). The removal of large proportions of megafauna assemblages, in particular, from marine systems can have cascading effects on other fisheries, the structure of communities and ecosystem function (e.g., Estes et al. 1998; Jackson et al. 2001; Pauly et al. 2003; Lewison et al. 2004; Myers et al. 2007). While anthropogenic impacts on marine megafauna can result from stressors such as noise and chemical pollution, boating and shipping activity, intensive tourism and coastal development (e.g., Ross et al. 2000; Laist et al. 2001; Williams et al. 2006; Hodgson and Marsh 2007; Smith et al. 2012), bycatch in fisheries is widely recognized as one of the most pressing threats to the persistence of many marine megafauna populations through the 21st century (e.g., DeMaster et al. 2001; Read 2008; Lewison et al. 2014; Trathan et al. 2014).

Major challenges associated with resolving the marine megafauna bycatch problem include that its causes are poorly understood, it is often poorly documented, and that it varies considerably between fishery types, the species or suite of species subject to bycatch, and even local conditions (Bache 2003; Marsh et al. 2003; Lewison et al. 2004; Cox et al. 2007). Bycatch can occur when marine megafauna do not perceive fishing gear (e.g., gill nets), when they are aware of the fishing gear but foraging around it on captured or discarded fish (e.g., trawl nets), or when gear is intentionally set around them (e.g., purse-seine nets – see below).

Most marine mammals, as well as some reptiles, birds and elasmobranchs, exhibit life history characteristics such as slow growth, late maturation and low reproductive rates, that render them vulnerable to population-level impacts from bycatch (Reeves et al. 2003; Read et al. 2006; Lewison et al. 2014). Since marine mammals share largely similar life history characteristics and, therefore, vulnerability to the impacts of bycatch, they form a logical grouping in terms of conservation, management and policy (Martin and Reeves 2002; Gales et al. 2003; Boyd et al. 2010). Between the 1970s and 1990s, some nations passed laws prohibiting the harm of marine mammals (e.g., Baur et al. 1999). They are afforded a high level of protection from human activities under national regulations in, for example: the United States, under the *Marine Mammal Protection Act* 1972; New Zealand, under the *Marine Mammals Protection Act* 1978; and Australia, under the *National Parks & Wildlife Act* 1974 and the *Environment Protection and Biodiversity Conservation (EPBC) Act* 1999. These laws have been introduced in recognition of the significant roles marine mammals play in ecosystems, the high aesthetic value they are given by at least some sections of society, and also in recognition of their cognitive abilities, the complex social societies in which they live and their considerable cultural and economic significance (Marsh et al. 2003).

In Australia, the *EPBC Act* was introduced, at least in part, to make provision for commercial fisheries to be assessed against criteria that went beyond the target species, i.e. to include evaluating the effects of fishing on other wildlife, the ecology of the ecosystem and environmental sustainability. Such provisions have also been adopted in some third party assessments of the sustainability of fisheries; for example, Principal 2 of certification by the Marine Stewardship Council entails assessment

against sustainability of the environment in which the fishery operates, including non-target species. Despite this recognition of the significance of marine mammals, bycatch in fisheries continues to be a major threat to most species (Reeves et al. 2013). For example, some cultures still hold a primarily utilitarian view of marine mammals; many developing nations lack the resources to assess, let alone mitigate against bycatch; and most species of marine mammals are subject to direct takes and/or bycatch in at least some parts of their geographic distributions (Whitehead et al. 2000; Read 2008). Indeed, many marine mammal species are still actively hunted or incidentally captured in fisheries within the very regions in which they fall under full protection from disturbance, harassment and takes as a result of human activities (Northridge and Hoffman 1999; Shaughnessy et al. 2003; Read 2008; Robards and Reeves 2011). For example, small cetaceans are still both actively hunted and incidentally caught in Peruvian artisanal fisheries, despite legal protection having been in place since the 1990s (Mangel et al. 2010).

Perhaps the most renowned case of public pressure leading to change in management and policy on fisheries interactions with marine mammals is the setting of tuna purse seine nets around dolphin schools in the eastern tropical Pacific Ocean. Some 500,000 dolphins per year were taken in the late 1960s and early 1970s, resulting in public outcry in the United States (e.g., Perrin 1969; Hammond 1981). A comprehensive observer program was implemented, bycatch levels were quantified, multi-stakeholder groups were established to seek solutions, and changes to fishing practices and policy ensued (Joseph 1994; Hall 1998). Although these interventions and changes in practice reduced dolphin bycatch dramatically (by two orders of magnitude), the dolphin populations impacted have not shown signs of recovery (e.g., Gerrodette and

Forcada 2005). This case exemplifies the complexity of the issue and highlights the vulnerability of populations with the life history characteristics of most marine mammals. The lack of recovery of spotted and spinner dolphin populations has been attributed to the under-reporting of dolphin bycatch, the ongoing effects of the chase and encirclement of dolphins on survival and reproductive output, and long-term changes in the ecosystem (Gerrodette and Forcada 2005; Wade et al. 2007; Cramer et al. 2008). This case also conveys the importance of estimating total fishing-related mortality for non-target species, which consists not only of the dead animals that are entangled/landed on deck (observed bycatch and accounted mortality), but also those that are caught/landed alive and then die post-release (observed bycatch, but unaccounted mortality), as well as those not retrieved or landed on deck, but dying after interaction with fishing operations (unobserved bycatch and unaccounted mortality, e.g., Jaiteh et al. 2014).

Over a decade ago, Marsh et al. (2003) outlined three outstanding problems in addressing marine mammal-fisheries interactions:

(1). Our understanding of the global extent and impact of interactions between marine mammal stocks and fisheries remains woefully inadequate,

(2). Even in countries where the scope of interactions is well understood, there is a lack of cooperation and common purpose between the agencies responsible for the management of fisheries and those with the mandate to manage marine mammals, and,

(3). Ecological interactions are particularly complex and it is still very difficult to determine the effects of fisheries harvests on the population biology of marine mammals.

At the time these issues were articulated, the bycatch of a number of protected species was also assessed in a trawl fishery off north-western Australia (Stephenson and Chidlow 2003). The protected taxa caught in this fishery included dolphins, turtles, sea snakes, sharks, sawfish, rays, seahorses and pipefish. The Department of Fisheries Western Australia (WA) implemented an independent observer program and proceeded with a variety of gear modification trials, focusing on reducing dolphin bycatch (e.g., Stephenson and Wells 2006). Small cetaceans interact with trawlers in many global locations, taking advantage of the concentrated food source by foraging on fish disturbed by the activity or discarded after catch sorting (e.g., Corkeron et al. 1990; Fertl and Leatherwood 1997; Svane 2005; Kovacs and Cox 2014). These foraging opportunities also present the risk of entanglement or otherwise becoming trapped, and negative outcomes for small cetaceans from interacting with trawl gear range from minor injuries to asphyxiation and mortality (e.g., Waring et al. 1990; Northridge et al. 2003, 2011).

1.1 Objectives

Evaluating the impact of an anthropogenic activity on any endangered, threatened or protected population requires knowledge of the scale of the impact (i.e., how many animals are being injured or killed); the size of the impacted population; and an assessment of the population's ability to absorb the human-induced mortality (e.g., Barlow et al. 1995; Wade 1998; Thompson et al. 2000; Read 2010). Population data for most small cetaceans around Australia, pelagic species in particular, are very limited, such that the conservation status of many species is listed as 'no category assigned' (Bannister et al. 1996; Ross 2006). Indeed, nothing is known of the abundance or life history characteristics of the dolphin population interacting with the

Pilbara Trawl Fishery. These identified gaps in our understanding of small cetacean populations, especially across remote north-western Australia (Allen et al. 2012), were used to frame the specific objectives of my Thesis, which are to:

1. Review the spatial and temporal patterns of dolphin bycatch in a north-western Australian trawl fishery, as reported in skippers' logbooks and independent observer records, and estimate total bycatch (Chapter 2);
2. Establish the species identity of the dolphins interacting with the Pilbara Fish Trawl Interim Managed Fishery and assess the population structure and connectivity of this population with adjacent populations using genetic methods (Chapter 3);
3. Estimate the abundance and fidelity of dolphins in the trawl fishery by conducting an aerial survey of the fishery and applying boat-based, individual dolphin photo-identification methods (Chapter 4); and,
4. Draw conclusions about acceptable levels of dolphin bycatch in this fishery based on the data presented and make recommendations for reducing dolphin bycatch and improving bycatch monitoring and mitigation (Chapter 5).

This research was initiated after an original approach to the Murdoch University Cetacean Research Unit from the Department of Fisheries WA to review the dolphin bycatch problem in the Pilbara region. Subsequently, funding was obtained from the Fisheries Research and Development Corporation of Australia, Department of Fisheries WA and commercial fishing industry (Nickol Bay Professional Fishers Association) to complete Objectives 2 and 3. Funding was later obtained from the Australian Marine Mammal Centre to complete Objective 4. Murdoch University provided the scholarship for the completion of this Thesis.

Chapter Two: Patterns of dolphin bycatch in a north-western Australian trawl fishery

2.0 Abstract

The bycatch of small cetaceans in commercial fisheries is a global wildlife management problem. Data from skippers' logbooks and independent observers were used to assess common bottlenose dolphin (*Tursiops truncatus*) bycatch patterns between 2003 and 2009 in the Pilbara Trawl Fishery, Western Australia. Both datasets indicated that dolphins were caught in all fishery areas, across all depths and throughout the year. Over the entire datasets, observer reported bycatch rates (n = 52 dolphins in 4,124 trawls, or 12.6 dolphins/1,000 trawls) were ca. double those reported by skippers (n = 180 dolphins in 27,904 trawls, or 6.5 dolphins/1,000 trawls). Generalised Linear Models based on observer data, which better explained the variation in dolphin bycatch, indicated that the most significant predictors of dolphin catch were: (1) vessel - one trawl vessel caught significantly more dolphins than three others assessed; (2) time of day – the lowest dolphin bycatch rates were between 00:00 and 05:59; and (3) whether nets included bycatch reduction devices (BRDs) - the rate was reduced by ca. 45%, from 18.8 to 10.3 dolphins/1,000 trawls, after their introduction. These results indicated that differences among vessels (or skippers' trawling techniques) and dolphin behaviour (a diurnal pattern) influenced the rates of dolphin capture; and that spatial or seasonal adjustments to trawling effort would be unlikely to significantly reduce dolphin bycatch. Recent skipper's logbook data show that dolphin bycatch rates have not declined since those reported in 2006, when BRDs were introduced across the fishery. Modified BRDs, with top-opening escape hatches from which dolphins might escape to the surface, may be a more effective means of

further reducing dolphin bycatch. The vulnerability of this dolphin population to trawling-related mortality cannot be assessed in the absence of an ongoing observer program and without information on trawler-associated dolphin community size, broader dolphin population size and connectivity with adjacent populations.

2.1 Introduction

Demersal trawl fishing for crustaceans, cephalopods and fish impacts benthic habitats and results in large quantities of incidental catch, or bycatch, of non-targeted species (Kennelly 1995; Pauly et al. 2002; Kelleher 2005). Trawling, gill netting and purse seining are the three largest causes of fisheries-related small cetacean mortalities worldwide (Northridge 1991; Read et al. 2006; Read 2008; Reeves et al. 2013). Entanglements in fishing gear and large-scale habitat modification have resulted in the extinction of the Yangtze river dolphin (*Lipotes vexillifer*), representing the first loss of a cetacean species directly attributable to human influences (Turvey et al. 2007). Several other populations and, indeed, species of small cetaceans, such as the Maui's dolphin (*Cephalorhynchus hectori maui*) of New Zealand's North Island and the vaquita (*Phocoena sinus*) of the Sea of Cortez, are at risk of extinction from the cumulative impacts of fishing related mortality and disturbance from gill netting and trawl fisheries (Perrin et al. 1994; Dawson et al. 2001; Jaramillo-Legoretta et al. 2007; Slooten 2013).

As a result of suspected and/or measured declines in dolphin populations due to fisheries bycatch, public concerns and pressure from non-government organizations, major changes in fisheries policy and practice have been implemented in several regions. After the introduction of the U.S. *Marine Mammal Protection Act* (MMPA)

in 1972, for example, high observer coverage and a variety of bycatch mitigation measures were implemented to quantify and reduce the bycatch of two dolphin species (spotted, *Stenella attenuata*, and spinner dolphins, *S. longirostris*) in the purse seine fishery for tuna in the eastern tropical Pacific (Hall 1998; Hall et al. 2000). Although massive reductions in dolphin capture rates were achieved, the impacted populations have not recovered (Lewison et al. 2004; Cramer et al. 2008).

New Zealand's Department of Conservation administers the *Marine Mammals Protection Act* of 1978. Numerous protected areas have been established, with time- and area-based restrictions placed on fishing activities that present high entanglement risks to marine mammals. One such protected area was established off the west coast of the North Island to reduce entanglements of the critically endangered Maui's dolphin. However, concerns remain over the efficacy of these measures, as gill netting and trawling are still allowed in certain areas (Slooten et al. 2006). Surveys of the distribution of the endangered Hector's dolphins (*C. hectori*) off the South Island suggest that restrictions on commercial gill netting protect 60% or less of the dolphin population for three months of the year (Rayment et al. 2011). New Zealand's endemic dolphin populations are predicted to continue declining under current management, driven primarily by ongoing bycatch in gill net and trawl fisheries (Slooten 2013).

All marine mammals in Australian waters are protected under the *Environmental Protection and Biodiversity Conservation Act* 1999. Fishers are required by legislation to report fatal and non-fatal entanglements of marine mammals to State and Commonwealth fisheries management agencies. The greatest threats to small

cetaceans in Australian waters are also associated with gill netting, purse seining operations and trawl fisheries (Shaughnessy et al. 2003). Here, the species most often affected by fishing mortality include: bottlenose (*Tursiops* spp.), common (*Delphinus delphis*), Australian snubfin (*Orcaella heinsohni*), Australian humpback (*Sousa sahulensis*) and spinner dolphins (Bannister et al. 1996; Ross 2006). Thousands of dolphins have died in commercial fishing operations over the past three decades (Ross 2006), the impacts of which are impossible to quantify without baseline data on the abundance and distribution of dolphin populations across the vast majority of Australian waters (Hamer et al. 2008). The tropical waters of north-western Australia are no exception, where numerous dolphin populations are exposed to commercial fishing, as well as large-scale habitat modification through the proliferation of the oil, gas and mining industries. No population estimates exist for any species in this region (Allen et al. 2012).

Trawl fisheries operate in many regions of Australian waters (Larcombe et al. 2006). The North West Shelf region of Western Australia (WA) has been trawled since the early 1970s, with the Taiwanese pair-trawl fishery catching in excess of 100,000 tons of fish, cephalopods and other invertebrates in the mid-1970s (Althaus et al. 2006). Catches declined to less than 10,000 tons per annum by the mid-1980s, when Chinese and Korean trawlers also fished the area and an experimental management regime was introduced (Sainsbury 1987). Shortly after this new regimen commenced, the foreign fleet diminished and a domestic fishery developed (Althaus et al. 2006). Since the early 1990s, catches in the Pilbara Trawl Fishery (PTF) have fluctuated between 2,000 and 3,500 tons per annum, dropping to <1,400 in the last five years, associated with a decline in trawl effort (Department of Fisheries 2013).

The bycatch of a number of protected species (dolphins, sea snakes, turtles and sawfish) in the PTF was first documented in 2002 (Stephenson and Chidlow 2003). A variety of bycatch mitigation techniques were pursued, focussed primarily on reducing dolphin bycatch (Stephenson et al. 2006; Department of Fisheries 2013). The efficacy of acoustic deterrents, or 'pingers', for reducing dolphin interactions with fisheries has continued to be evaluated in this and other regions, with inconsistent results depending on the dolphin species involved, type of fishery and the type and number of pingers deployed (Dawson et al. 2013). Pingers proved ineffective in deterring bottlenose dolphins from interacting with trawl gear in the PTF (Stephenson and Wells 2006). Field trials of bycatch reduction devices (BRDs) resulted in a reduction in the number of dolphins landed on deck and they were made compulsory across the fishery in March 2006 (Stephenson et al. 2006).

The dolphins subject to bycatch in the PTF are common bottlenose dolphins (*T. truncatus*, 'bottlenose dolphins' hereafter) (Allen and Loneragan 2010), a globally widespread species, occurring in tropical and temperate latitudes (Rice 1998). Bottlenose dolphins are thought to be widely distributed in Australian pelagic waters (Ross 2006; Hale 2008), mixing with and/or being replaced by Indo-Pacific bottlenose dolphins (*T. aduncus*) in shallow, coastal areas, including those of north-western Australia (Allen and Loneragan 2010; Allen et al. 2012). In the Action Plan for Australian Cetaceans, bottlenose dolphins are listed as 'no category assigned because of insufficient information' (Bannister et al. 1996) and very little is known of the populations off north-western Australia or, indeed, any pelagic population around Australia. Due to this broad lack of even baseline data, assessments of the status of individual bottlenose dolphin stocks, or populations, are not yet possible.

Previous studies in the PTF by the Department of Fisheries WA have been based primarily on trialling the efficacy of pingers (Stephenson and Wells 2006) and various BRDs (Stephenson et al. 2006) in reducing dolphin bycatch. While some aspects of the geographical and temporal nature of incidental dolphin captures were evaluated, these assessments were based on data collected during ca. six- and 18-month trials between 2004 and 2006 (Stephenson and Wells 2006; Stephenson et al. 2006). Here, six years of data from skippers' logbooks and independent observer records collected from August 2003 until September 2009 were used to build upon this earlier research and investigate the spatial and temporal patterns of dolphin bycatch across the PTF. The aims were, firstly, to assess the spatial, daily and seasonal data on fishing effort and dolphin bycatch, and secondly, to evaluate the effectiveness of different net designs (those with and without BRDs) in reducing dolphin bycatch.

2.2 Materials and Methods

2.2.1 Characteristics of the Pilbara Trawl Fishery

The PTF, within the broader Pilbara Demersal Scalefish Fishery (which also includes trap and line fisheries), is bound by longitudes of 116° to the west and 120° to the east, and by an approximation of the 50 m depth contour to landward and the 100 m depth contour to seaward (Fig. 2.1). Since being gazetted in 1998, four Management Areas have been open to trawling, comprising a total fishing area of ca. 23,000 km^2 (6,900 nm^2). The equivalent of 4.3 full-time vessels operated year-round in the PTF between 2003 and 2009, with slightly reduced effort from December to March when cyclones are more frequent. The trawlers generally stay at sea for five to 12 days at a time, fishing throughout the day and night. Individual trawls ranged in duration from 30 min to five h, with a median trawl time of ca. 2.7 h.

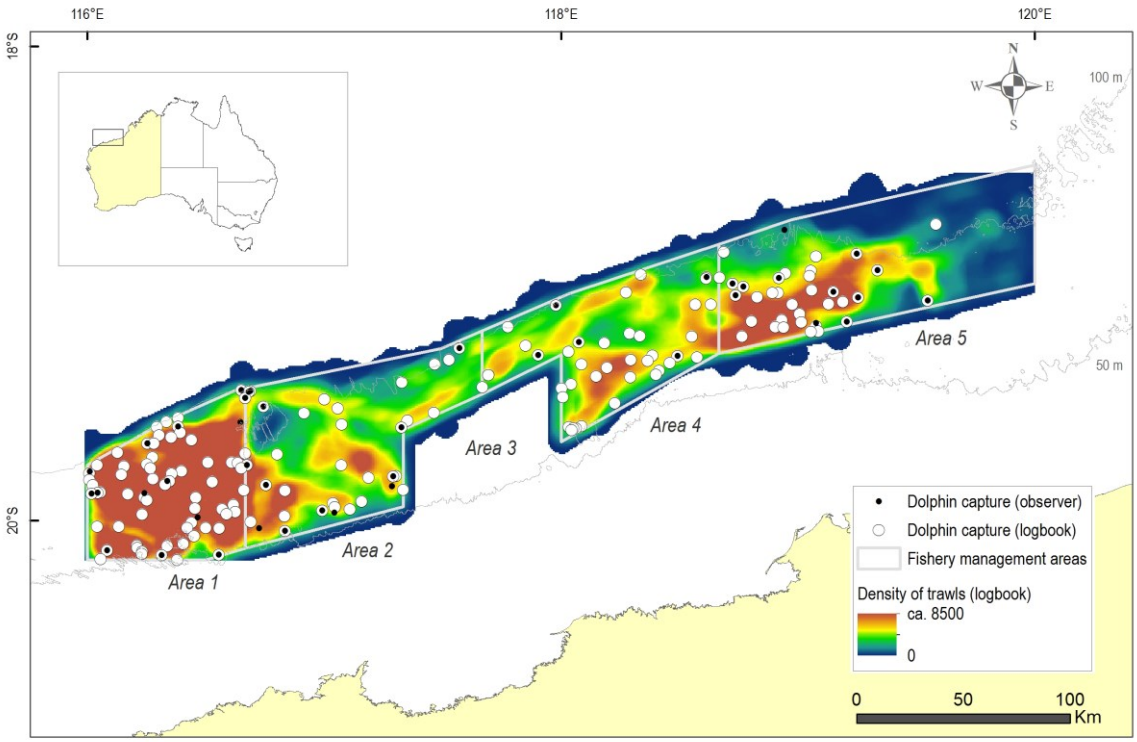

Figure 2.1. The Pilbara Trawl Fishery off the north-western coast of Australia. Figure includes: a) the 50 and 100 m depth contours; b) the boundaries of the fishery management areas (Areas 1, 2, 4 and 5; Area 3 in the central southern region of the fishery is closed to trawling); c) the spatial density of fishing effort based on logbook trawls; and d) the location of dolphin bycatch events reported in skippers' logbooks and by independent observers (August 2003 to September 2009).

The total trawling effort ranged from 4,500 to 6,000 trawls (ca. 11,000 to 16,000 h) per annum (Table 2.1) between 2003 and 2009, though it has averaged ca. 9,000 h per annum from 2010 to 2012 (Department of Fisheries 2013).

Data for this fishery are reported in three different 12-month intervals: The annual State of the Fisheries reports by the Department of Fisheries summarise data from January to December (calendar years); skippers' logbook data are summarised from July until the following June (Australian financial years) by industry for the Australian Taxation Office; and observer records for the fishery were summarized

from October to September. In this study, data from the Department of Fisheries have been presented by calendar years for ease of comparison, but the analyses of logbook and observer data were based on the industry format of the financial year (Table 2.2).

Table 2.1. Total numbers of trawl days, hours and individual trawls in the PTF. Numbers refer to those conducted by calendar year (January to December) in the Pilbara Trawl Fishery from 2003 until 2009 (source = Department of Fisheries 2013). *Not all data for calendar year provided. These figures represent the subset subject to analyses, not the annual totals.

Year	Trawl days	Trawl hours	Trawl numbers
2003	1,014	14,663	1,107*
2004	953	15,372	5,591
2005	886	14,721	5,500
2006	914	15,792	5,882
2007	841	14,197	5,204
2008	831	11,966	4,533
2009	713	10,605	2,845*

Trawl vessels in the PTF tow a single net at a speed of ca. three to three and a half knots (5.6–6.5 km/h), with twin otter boards maintaining the net spread (see also Jaiteh et al. 2013). Most nets in the PTF consist of four main sections: the wings, which form the opening or mouth of the net; the belly and neck, which are immediately behind the mouth of the net and where the net tapers; the extension, a tubular section; and the codend, where the catch is collected (Fig. 2.2). The diameter and mesh size decrease in each panel with distance from the opening of the net. The length of the head rope must not exceed 36.6 m, while the total length of the net, including cables, sweeps and bridles, is limited to 274.3 m. The footrope is weighted and contains bobbins (<35 cm in diameter) that are spaced about 30 cm apart and roll along the sea floor.

Nets used in the PTF consist of diamond mesh. The first section of the net belly measures 4.8 m in length when the net is stretched. In October 2008, the belly and neck sections of the nets were shortened to allow for a shorter escape route for dolphins that enter the net and interact with the exclusion grid (Fig. 2.2). Based on stretch mesh measurements, the nets are approximately 44 m long from the footrope to the start of the codend and, when trawling/fishing, they are likely to be about 60–70% of this length.

Bycatch exclusion grids and escape hatches were trialled in 2004 and 2005, then fitted into all nets used in the PTF in March 2006 (Stephenson and Wells 2006; Stephenson et al. 2006). The BRDs in use at the time of this study consisted of a semi-flexible metal grid and a bottom-opening escape hatch (through which large animals could leave the net), with a loose skirt of netting to prevent the loss of target species covering the hatch (see also Jaiteh et al. 2013). The exclusion grid was held upright by a number of floats. The grid lay at an angle with the float-equipped top section anterior to the lower section, so that bycatch and benthos were deflected down toward the bottom-opening escape hatch.

In June 2008, the BRDs were moved forward in the net, from just before the codend, to the start of the net extension. This was done to prevent dolphins from backing down into the extension and to provide a shorter escape route between the BRDs and the opening of the net. All grids featured vertical bars made of stainless tube and central sections of braided stainless wire.

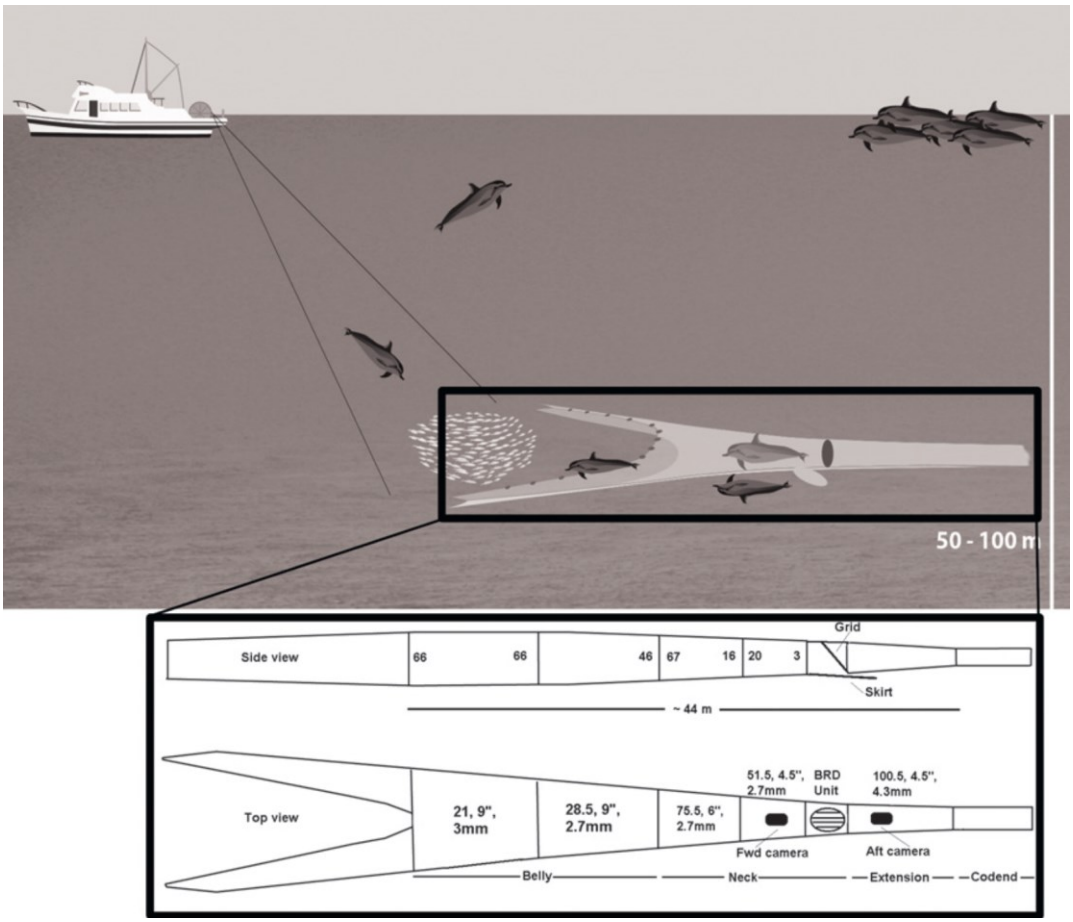

Figure 2.2. Schematic of trawler and trawl net on or near the seabed. Also illustrated are the typical positions of dolphins in and around the net, as well as following the trawler on the surface. The detailed net diagram represents the typical net specifications used in the Pilbara Trawl Fishery in 2008 and 2009, showing the side and top views, location of the Bycatch Reduction Device and the skirt covering the escape hatch. The lengths of the different panels are given as number of meshes, mesh length (in inches) and diameter of twine (in mm). In the side view, the height of each panel is given as the number of meshes. Diagram not to scale. Modified from Stephenson et al. (2006) and Jaiteh et al. (2013) following plans by H. McKenna for the 'Magnet Box Diamond Net' with short neck.

The trawl data were categorised into three broad net types: 1) before the introduction of the BRDs (August 2003 until February 2006; excluding the BRD trials) – ''No BRD''; 2) BRD trials from the previous period, after the compulsory introduction of the BRDs and before they were moved forward (primarily March 2006 to May 2008)

– ‘‘BRD’’; and 3) after the BRDs were moved forward in the net (June 2008 until September 2009) – ‘‘BRD forward’’. The total number of trawls, number of dolphin bycatch events and dolphin catch rate per 1,000 trawls were calculated for each category (Table 2.2).

Table 2.2. Dolphin bycatch rates reported by skippers and observers. Number of dolphins caught, number of trawls observed, and dolphin bycatch rate/1000 trawls in Australian financial years of July to June (as per presented by industry in logbooks) and divided by net type (i.e. No BRD, after the introduction of BRDs, and then BRDs being moved forward in the extension).

Period	**Skippers' logbook**			**Independent observer**		
	# dolphins	**# trawls**	**#/1,000 trawls**	**# dolphins**	**# trawls**	**#/1000 trawls**
a) No BRD						
Aug03-Jun04	19	3,373	5.6	1	46	21.7
Jul04-Jun05	48	4,793	10.0	9	481	18.7
Jul05-Feb06	32	3,002	10.7	10	537	18.6
Total No BRD	99	11,168	8.9	20	1,064	18.8
b) BRD						
Jan05-Feb06	5	854	5.9	3	298	10.1
Mar06-Jun06	9	1,569	5.7	7	657	7.6
Jul06-Jun07	31	5,345	5.8	10	1,055	9.5
Jul07-May08	16	3,871	4.1	5	429	11.7
Total BRD	61	11,639	5.2	25	2,439	10.3
c) BRD forward						
Jun08-Jun09	18	4,365	4.1	7	621	11.3
Jul09-Sep09	2	732	2.7			
Total BRD forward	20	5,097	3.9	7	621	11.3
d) BRD + BRD forward						
Jan05-Sep09	81	16,736	4.8	32	3,060	10.5
TOTAL	**180**	**27,904**	**6.5**	**52**	**4,124**	**12.6**

2.2.2 Data analyses

The skippers' logbook and independent observer data from October 2003 to August 2009 for the PTF were provided by the Department of Fisheries and stored in a Microsoft Access database. The skippers' logbook data for this period of trawl fishing activity comprised information on targeted catch and bycatch from 30,684 trawls and the observer data set contained similar details from 4,939 trawls. Structured query language (SQL) queries were written to filter the dolphin bycatch data and location data were examined in ArcGIS. Summary figures and binary logistic generalised linear models were run in SPSS 16.01.

Excel files containing latitudes and longitudes of trawls were used to create point files in ArcGIS. The start and end latitudes and longitudes were combined using the Merge function and used to calculate the straight-line distance (line segment) of each trawl (in nautical miles, nm). Data were screened for trawls that were either outside the trawling management areas and/or line segments longer than 21 nm (39 km, equivalent to a trawl duration of about six to eight h). Trawls largely outside the management areas, or of greater than 2.2 times the distance and/or duration of the median trawl time (2.7 h), were considered outliers not representative of normal fishing operations or, more likely, the result of human error in data entry. After removing these data, along with duplicate records and those with missing values, ca. 90% of the logbook data (or n~11,200 trawls for the No BRD net type, ~11,700 for the BRD net type and n~5,100 trawls for the BRD forward category) and 85% of observer data remained for further analyses. The density of lines (trawls) was calculated using the Line Density function in ArcGIS.

As with net type, each of the trawl variables used in the analyses were placed into the following categories: Time of day (morning {06:00–11:59}/afternoon {12:00–17:59}/night {18:00–23:59}/early morning {0:00–05:59}); Area (1/2/4/5, fishery management area 3 is closed to trawling); Season (wet {December–April}/dry {May–November}); Vessel (1/2/3/4); Trawl duration (0.1–1.0 h/1.1–2.0 h/2.1–3.0 h/3.1–4.0+ h); Trawl distance (0.1–5.0 nm/5.1–10.0 nm/10.1–15.0 nm/15.1–20.0 nm); Trawl depth (51–60 m/61–70 m/71–80 m/81–90 m/91–100+ m); and dolphin bycatch (present/absent).

2.2.3 Binary logistic generalised linear models

The categorical variables net type, time of day, management area, season, vessel and trawl duration were fitted as individual predictors for the presence of dolphin bycatch in separate binary logistic generalised linear models (GLMs) (Quinn and Keough 2002) for the logbook data and the observer data. These models were used to determine which variables were significant in predicting the presence of dolphin bycatch. The unit of measure for the presence of dolphin bycatch was the individual trawl and each is assumed to be independent. The significant predictors, and the interactions between them, were then used in combination in multi-predictor binary logistic GLMs. The multi-predictor GLMs were used to determine which combination of predictors accounted for the highest probability of the presence of dolphin bycatch. Akaike's Information Criterion (AIC) (Akaike 1974), which selects the most parsimonious model that best fits the data by taking into account the variation explained and the number of terms in the model, was used to select the best model. The lower the AIC value, the better the fit of the model (Burnham and Anderson 2002).

Given the relatively low number of trawls in the observer data set for the BRD and BRD forward net categories, the data for these categories were pooled into a BRD category for No BRD versus BRD comparisons. For ease of comparison with earlier bycatch mitigation research by the Department of Fisheries (Stephenson and Wells 2006; Stephenson et al. 2006), the results of dolphin capture rates under the various conditions assessed are presented in dolphin captures per 1,000 trawls.

2.2.4 Independent observer coverage levels

After the introduction of BRDs across the PTF in March 2006, scientific advice from within the Department of Fisheries suggested that minimum observer coverage from 2006–2007 onward should be at least 22% of total fishing effort and be representative of the operations of the fishery (Stephenson et al. 2006). Observer coverage rates were calculated in Australian financial years from the datasets provided. The sample size of trawls that should be monitored by observers to obtain an estimate of dolphin bycatch rates with a relative proportional standard error (Coefficient of Variation) of 20% was also calculated. Standard estimation equations for a population total based on simple random sampling from a finite population were used (Thompson 2002).

2.3 Results

2.3.1 Overall dolphin bycatch rates

The total number of trawls for a full calendar year in the PTF data provided was highest in 2006 (5,882 trawls; 15,792 h of trawling) and lowest in 2008 (4,533 trawls; 11,966 h of trawling). In total, 171 dolphin capture events, involving 180 dolphins, were recorded in the skippers' logbook data of 27,904 trawls from 2003 to 2009, at an

overall rate of 6.5 dolphins/1,000 trawls (Table 2.2). Observers reported 48 dolphin capture events, involving 52 dolphins, in the observed subset of 4,124 trawls at an overall rate of 12.6 dolphins/1,000 trawls (Table 2.2). Note, however, that the dolphin bycatch rates varied among the broad categories of net type and were lower after Bycatch Reduction Devices (BRDs) were installed (Table 2.2, see also below).

In general, a single dolphin was caught in the net, except on nine occasions in which skippers reported two dolphins caught in one trawl and four occasions in which observers reported two dolphins caught in one trawl. These multiple capture data were too sparse to model actual counts, so the presence of a dolphin bycatch event ('at least one dolphin caught') was the measure used for the generalised linear models. Underwater video observations of dolphins in 44 operating trawls (ca. 1% of 2008–2009 effort) found that one or two dolphins typically swim inside the actively fishing trawl nets at a time, although up to nine dolphins have been recorded in the net at any one time (Jaiteh et al. 2013).

2.3.2 Spatial dolphin bycatch and fishing effort

The spatial distribution of lines, representing trawls from August 2003 until September 2009, indicated that fishing effort was most intense in Management Area 1 and least intense in the most remote (in terms of distance from home ports) northern and eastern regions of Management Area 5 (Fig. 2.1). The catch of dolphins appeared largely to reflect the intensity of fishing effort, with most dolphins captured in Area 1 (Fig. 2.1). From the logbook data, dolphin capture rates were greatest in Management Area 4, but for observer data, they were highest in Area 2. These differences in dolphin catch rates among areas were, however, not significant (Table 2.3).

Table 2.3. Presence of dolphin bycatch by individual factors. Results from binary logistic generalised linear models to predict the presence of dolphin bycatch in trawl nets by individual factors, based on skipper logbook data and independent observer data (skipper logbook number of trawls, n = 27,914; independent observer, n = 4,178, except for the predictor trawl duration, where logbook n = 27,489 and observer n = 4,153). df = degrees of freedom. Net type (separate) = analysis of three net types (No BRD, BRD, BRD forward). Net type (pooled) = analysis of two net types (data for BRD and BRD forward pooled).

Factor		**Skipper logbook**		**Independent observer**	
	df	**Likelihood ratio (χ^2)**	***P***	**Likelihood ratio (χ^2)**	***P***
Time of day	3	44.03	<0.001	8.39	0.039
Net type (separate)	2	18.18	<0.001	5.18	0.075
Net type (pooled)	1	17.89	<0.001	5.06	0.025
Vessel	3	8.20	0.042	11.76	0.008
Trawl duration*	3	12.22	0.007	3.48	0.323
Trawl area	3	3.95	0.267	2.87	0.413
Season	1	0.01	0.904	0.34	0.853

2.3.3 Predictors of dolphin bycatch

Binary logistic generalised linear models fitting single predictors found that vessel, net type (BRD and BRD forward pooled), and time of day were each significant in predicting the occurrence of dolphin bycatch in the PTF for both the skippers' logbook and observer data (Table 2.3). Trawl duration was also a significant predictor in the logbook data only (higher bycatch rates in longer trawls). In contrast, management area and season (wet versus dry) were not significant in predicting the occurrence of dolphin bycatch (Table 3). For the independent observer data, only vessel, time of day and net type (BRD and BRD forward pooled) were significant in predicting the occurrence of dolphin bycatch (Table 2.3). Rates of dolphin bycatch were significantly higher in one vessel than the other three and capture rates were significantly lower in the early morning than at other times of the day (Fig. 2.3A and

2.3B). While the magnitudes of dolphin capture rates were consistently higher for the observer than the logbook data, they followed a similar pattern of change for each factor (Fig. 2.3A and 2.3B, Table 2.3). The predicted dolphin capture rates did not differ significantly between different trawl durations, trawl distances, seasons or between depths (Table 2.3).

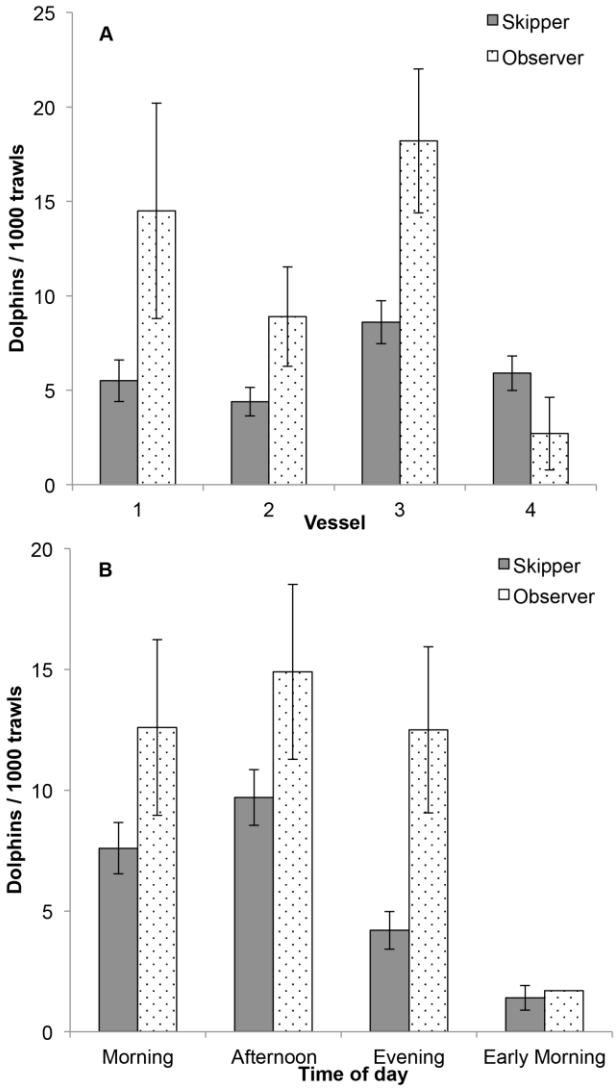

Figure 2.3. Dolphin bycatch rates by A) vessel and B) time of day. Mean (±1 SE) dolphin bycatch rates by A) vessel (1-4) and B) time of the day (Morning = 06:00–11:59; Afternoon = 12:00–17:59, Evening = 18:00–23:59; Early Morning = 00:00– 05:59) in the Pilbara Trawl Fishery. For skipper logbook, n = 27,914; for independent observer, n = 4,178.

The mean rates of dolphin bycatch differed markedly between skippers' logbooks and observer reports. Observer reported dolphin bycatch rates were 2.1, 2.0 and 2.9 times higher than those from logbooks in the No BRD, BRD and BRD forward periods of trawling activity, respectively (Table 2.2; Fig. 2.4). The number of observed trawls for the BRD forward category (n= 621) was much lower than in the prior two periods (n= 1,064 and 2,439, respectively). Observer reported catch rates were 2.2 times higher than the logbook reported rates in the BRD and BRD forward pooled category. After the introduction of BRDs, the rate of dolphin bycatch from both the skipper and observer records declined by ca. 45% (Fig. 2.4). After the BRDs were moved forward in the nets, the logbook data showed a further slight decline in dolphin capture rates and the observer data indicated a slight increase in dolphin catch rates (Table 2.2; Fig. 2.4).

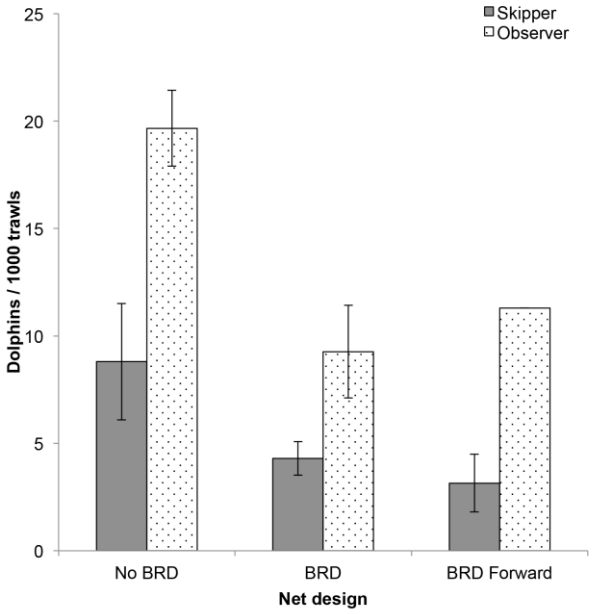

Figure 2.4. Dolphin bycatch rates by differing net design in the Pilbara Trawl Fishery. Mean (±1 SE) dolphin bycatch rates by differing net designs. BRD = BRD fitted just forward of the codend and at the aft end of the tubular net extension; BRD forward = BRD moved to the forward end of the extension.

From the skippers' logbook data, time of day, net type and vessel were significant in predicting dolphin bycatch, as was the net type-vessel interaction, although the effect was not nearly as strong as the main factors (Tables 2.4a and 2.5a). This interaction was due to the fact that dolphin capture events were lower in the BRD than No BRD net type category for three vessels, but remained the same for one vessel (Fig. 2.5). For the independent observer data, vessel and time of day were the strongest predictors of dolphin bycatch, while the net type effect was close to significance (P = 0.06, Tables 2.4b and 2.5b).

Table 2.4. Summary of full models to predict dolphin bycatch by fitting multiple factors for a) skippers' logbook data and b) independent observer data. Results from binary logistic generalised linear models for predicting the occurrence of dolphin bycatch in the Pilbara Trawl fishery using time of day, net type, vessel and the net type x vessel interaction as predictors from a) skipper logbook data (number of trawls, n = 27,914) and b) observer data (n = 4,178).

Full models	**df**	**Model Log-likelihood**	**Likelihood ratio (χ^2)**	**P**
a) Skippers' logbook data				
$\beta_0 + \beta_1 V1 + \beta_2 V2 + \beta_3 V3 + \beta_4 TOD1 + \beta_5 TOD2 + \beta_6 TOD3 + \beta_7 NT1 + \beta_8 (V1*NT1) + \beta_9 (V2*NT1) + \beta_{10} (V3*NT1)$	10	-54.08	82.63	<0.001
b) Independent observer data				
$\beta_0 + \beta_1 V1 + \beta_2 V2 + \beta_3 V3 + \beta_4 TOD1 + \beta_5 TOD2 + \beta_6 TOD3 + \beta_7 NT1$	7	-35.89	24.27	0.001

Table 2.5. Model comparison with the full model (Table 2.4) for predicting dolphin bycatch by fitting multiple predictors for a) skippers' logbook data (number of trawls, n = 27,914) and b) independent observer data (n = 4,178). Compares the full model with the reduced model to indicate the significance of the additional predictors.

Predictors	**df**	**Likelihood ratio (χ^2)**	***P***
a) Skippers' logbook data			
Intercept	1	33323.66	<0.001
Time of day (*TOD*)	3	46.99	<0.001
Net type (*NT*)	1	15.15	<0.001
Vessel (*V*)	3	12.58	0.006
Net type * Vessel	3	8.57	0.035
b) Independent observer data			
Intercept	1	3375.33	<0.001
Vessel (*V*)	3	11.05	0.011
Time of day (*TOD*)	3	8.89	0.031
Net type (*NT*)	1	3.49	0.062

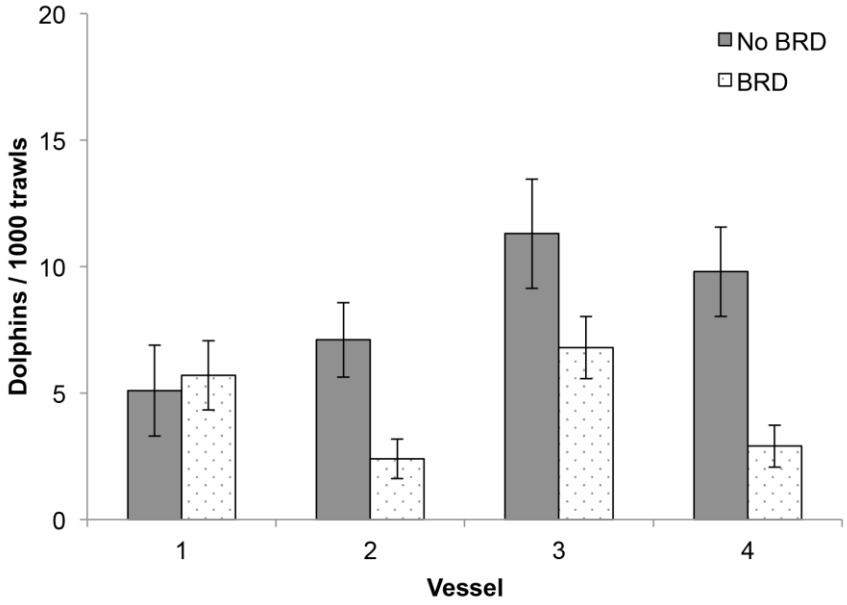

Figure 2.5. Dolphin bycatch rates net type x vessel interaction. Mean (±1 SE) dolphin bycatch rates illustrating the net type (No BRD vs BRD) x vessel (vessel 1-4) interaction based on skipper's logbook data.

2.3.4 Independent observer coverage levels

From the 2003–2009 data provided for this study, the overall observer coverage was ca. 16%. Observer coverage levels attained after the 22% minimum was recommended by internal Department of Fisheries scientific advice were 17% in 2006–2007, 13% in 2007–2008, 13% in 2008–2009 and ca. 8% from July to September 2009.

Given a ‘‘population’’ of 3,000 trawls (six-eight months of trawling in the PTF), with a dolphin bycatch rate of 20 dolphins/1,000 trawls (roughly equivalent to the rate reported by observers prior to the introduction of BRDs – see Table 2.2), about 30% observer coverage would be required in order to estimate bycatch rates with a relative proportional standard error of 20%. For dolphin bycatch rates of 10 dolphins/1,000 trawls (approximating the rate reported by observers after the introduction of BRDs), 46% of the 3,000 trawls would need to be monitored and, for five dolphins/1,000 trawls (the rate reported by skippers after the introduction of BRDs), 62% of the 3,000 trawls would need to be observed.

2.4 Discussion

In this study, detailed, long-term catch and effort data from the Pilbara Trawl Fishery were evaluated to assess patterns of dolphin bycatch and determine whether the introduction of spatial and/or temporal fishery management measures might contribute to mitigating dolphin bycatch. The aim was also to quantify differences in dolphin bycatch rates by net type. In general, the trends in dolphin bycatch rates from skippers’ logbooks and independent observer datasets followed similar patterns of variation with vessel, time of day and the net type (with or without Bycatch Reduction

Device) in use. The reported rates of dolphin capture from the logbooks were consistently lower (<½) than those reported by observers. This is consistent with the reporting of bycatch in a number of other fisheries; particularly where the capture of marine mammals is illegal (e.g., Read et al. 2006; Moore et al. 2010). Assuming the number of dolphin capture events reported in the 2010–2012 logbooks (Department of Fisheries 2011, 2013) was ca. ½ the number observers would have reported, had an observer program continued after 2009, a minimum of ca. 500 bottlenose dolphins were caught in the PTF in the decade 2003–2012.

The analysis of dolphin bycatch patterns on spatial, daily and seasonal scales, and comparisons among different net designs, contradicted some of our expectations. For example, the greatest source of variation was not the net type (No BRD vs BRD/BRD forward). Most of the variation in dolphin bycatch was explained by the predictor variables of vessel and time of day. In the full model, net type was significant for the skippers' data and close to significance for the observer data. While the logbook data was a much larger dataset (ca. seven times more trawls than the observer dataset), the observer data better explained variation in dolphin bycatch, perhaps because skippers missed some bycatch events (i.e. when dolphins fell out of the bottom-opening escape hatch on winch-up and prior to being landed on deck). Accordingly, most of the discussion focuses on the results from the observer data.

2.4.1 Temporal patterns of dolphin bycatch and fishing effort

Observer reported dolphin catch rates in the six-hour period of early morning (00:00–05:59), when the least fishing occurs, were up to 85% lower than in the other three 6 h periods of the day. Logbook records also indicated a similar pattern, although the

difference between periods was not as marked as those from the observer data. This result is reasonably consistent with the smaller subset of data summarised by Stephenson and Wells (2006). Bycatch records collected between January 2004 and June 2005 indicated that 92% of dolphins were caught between 7am and 8pm (Stephenson and Wells 2006). It is difficult to determine why dolphins might be less likely to be caught in the late evening and early morning. Bottlenose dolphins were seen foraging around the trawlers in the PTF throughout the day and night (pers. obs.), though it was not possible to determine if this occurred to the same extent at night as it did during the day.

Bottlenose dolphins (*Tursiops* spp.) also foraged around trawlers throughout the day and night in Moreton Bay, Queensland (Chilvers and Corkeron 2001), and Spencer Gulf, South Australia (Svane 2005). In a study of two fisheries off the north-eastern United States, Waring et al. (1990) noted that the bycatch of common dolphins (*Delphinus* sp.) and pilot whales (*Globicephala* sp.) tended to follow a diel pattern, with common dolphins being caught at night and pilot whales caught during the day.

Bottlenose dolphins interacting with trawlers in the PTF may have adopted a diurnal pattern of behaviour in response to this foraging association, just as the behavioural budgets and social structure of bottlenose dolphins have adapted to other circumstances in which anthropogenic activities mediate a particular schedule or regimen (Shane et al. 1986). Numerous studies have demonstrated the adaptability of bottlenose dolphin behaviour to human activity, for example: dolphins spent less time in Milford Sound, New Zealand, during periods of intense tour boat activity (Lusseau 2005); free-ranging dolphins adopt a daily activity pattern to take advantage of

provisioning by tourists in Shark Bay, Western Australia (Smith et al. 2008); and artisanal fishing in Laguna, Brazil, and trawl fishing in Moreton Bay, Queensland, have documented influences on the activity budgets and association patterns of bottlenose dolphins (Chilvers and Corkeron 2001; Ansmann et al. 2012a; Daura-Jorge et al. 2012). This rapid learning ability and behavioural flexibility means that the chances of dolphins interacting with boats and fishing gear are greatly increased, particularly when food is an incentive (Donaldson et al. 2010).

Underwater video data collected in daylight hours suggest that dolphins spend considerable time foraging in and around trawl nets in the PTF (Jaiteh et al. 2013). If this foraging effort is sufficient to procure their daily food requirements, the dolphins may be less inclined to do so late at night and in the early morning, opting instead to forage less and remain vigilant against predation. Known predators of dolphins, such as sandbar (*Carcharhinus plumbeus*), oceanic white tip (*C. longimanus*) and tiger (*Galeocerdo cuvier*) sharks, also follow trawlers in the PTF (pers. obs.). Dolphins have been shown to modify their habitat use in response to the presence of tiger sharks (Heithaus and Dill 2007). Regardless of the reasons behind the lower bycatch rate in the early mornings, a restriction of fishing activity in the daytime and concomitant increase at night would be unlikely to reduce dolphin bycatch rates in the medium- to long-term, as the dolphins may be able to adapt their behaviour to this change in fishing activity.

Both skippers' logbook and independent observer data suggested that season had little influence on the likelihood of dolphin bycatch in the PTF. Although relatively little is known of the ecology and movements of bottlenose dolphins interacting with the

PTF (but see Jaiteh et al. 2013) or, indeed, those in any of Australia's extensive pelagic waters (Ross 2006), this lack of an effect is not surprising. Prevailing winds and rainfall levels do change on a seasonal basis in this region, but there are no marked changes in the physical or biological conditions (such as water temperature or prey abundance/density) in the pelagic environment that might be expected to result in seasonal fluctuations in the numbers of dolphins in the area. Furthermore, underwater video footage, photographic identification and genetic evidence indicates that at least some individual dolphins show fidelity to foraging around trawlers for periods of weeks to years (Allen and Loneragan 2010; Jaiteh et al. 2013).

2.4.2 Vessel and net type effects on the probability of dolphin bycatch

A strong vessel effect was evident in both the logbook and observer data, and in both single- and multi-predictor generalized linear models (GLMs). One vessel had higher bycatch rates than the other three assessed. The difference in dolphin catch rates among vessels is difficult to interpret, especially given the similarities in boat configurations and nets in this small fishery. It may be attributable to the different fishing practices employed by different skippers in the fleet. For example, some skippers tend to conduct their fishing operations in a very consistent manner over time, while others tend to modify how they are fishing on a frequent basis. Furthermore, some skippers tend to take more risks than others in terms of trawling over or near benthic structures, such as rocky reefs or pipelines associated with the offshore oil and gas industry. It is likely that more consistent trawling, and therefore fewer instances of rapid winch-up or net collapse, results in fewer dolphin captures.

Net type (No BRD vs BRD vs BRD forward) was also significant in predicting dolphin bycatch in the single and multi-predictor GLMs using the skippers' logbook dataset. In the observer data, net type (No BRD vs BRD/BRD forward pooled) was significant in the individual model, and close to significance in the multi-predictor model. The relatively small sample size of observer coverage for the BRD forward design, along with the relatively low incidence of reported dolphin catch rates, reduced the power to detect any change/effect among the three net designs in the observer data. Differences in skipper behaviour and detail of reporting dolphin bycatch are likely to account for the interaction detected between vessel and net type detected in the skippers' logbook dataset.

Both the skipper and observer reported rates of dolphin bycatch dropped by ca. 45% after the introduction of BRDs, consistent with the earlier assessment of the smaller subset of data (Stephenson et al. 2006). The trends after the forward movement of the BRDs, however, were inconsistent between skipper (a slight further decrease in dolphin catch rates) and observer data (a slight increase) and no significant changes were detected in either dataset. Exclusion grids and escape hatches of various forms have been trialled to reduce bycatch of marine mammals, turtles and other megafauna in numerous trawl fisheries around Australia and the world. While detailed measures of their efficacy, including long-term follow-up, are scarce, those that have met with some success include the following: Northridge et al. (2005) have experimented with exclusion grids and top-opening escape hatches in an English pelagic bass pair-trawl fishery, reporting reductions in common dolphin bycatch without the loss of target species; Zeeberg et al. (2006) report on the use of escape hatches to reduce the

bycatch of a number of species of small cetaceans and other megafauna in the Dutch trawl fleet fishing off Mauritania; top-opening escape hatches and exclusion grids have reduced the bycatch of turtles, large sharks and rays in Australia's Northern Prawn Fishery (Brewer et al. 2006); the bycatch and mortality rates of fur seals (*Arctocephalus* spp.) were reduced with the use of large, bottom-opening escape hatches in a pelagic, mid-water trawl fishery off Tasmania (Lyle and Willcox 2008).

Since the reported reduction in dolphin bycatch rates in the PTF after the introduction of BRDs in early 2006 (this study; Stephenson et al. 2006), annual fishing effort has declined by ca. 35% (2006 = 15,792 h; 2012 = 10,269 h) (Department of Fisheries 2013). According to the latest skippers' logbook data, however, dolphin bycatch rates have increased above those reported immediately after the BRDs were made mandatory (2006 =2.2 dolphins/1000 h trawling; 2012= 2.8 dolphins/1000 h trawling) (Department of Fisheries 2013). This minimum estimate, combined with underwater video footage showing a proportion of incidentally caught megafauna falling out of the bottom-opening escape hatch before being landed on deck (Allen and Loneragan 2010), indicates that bycatch rates reported in both skippers' logbooks and observer records are invariably underestimates and that BRDs are unlikely to be as effective as first presumed. Similarly, in South Australia, an unknown proportion of endangered Australian sea lions (*Neophoca cinerea*) sustain life-threatening injuries or die in gill nets and drop out before being detected, even by vigilant onboard observers (Hamer et al. 2011; 2013). Furthermore, bottom-opening escape hatches are not well suited to dolphins and other air-breathing animals in the PTF, which tend to swim upward and push on the upper ceiling of the net (in an attempt to get to the surface) when trying to escape (Allen and Loneragan 2010).

2.4.3 Spatial patterns of dolphin bycatch and fishing effort

Logbook data suggested that dolphin capture rates were highest in Management Area 4 of the PTF, while observer data indicated the highest rate was in Area 2. These differences were not significant in predicting dolphin capture in either single- or multi-predictor GLMs based on observer data. Nor were there any marked differences in capture rates by depth in the logbook or observer data. These results, based on six years of data, corroborate the earlier study by Stephenson and Wells (2006) from an 18-month subset of data and are to be expected, due to the broad extent of interactions between dolphin and trawlers operating in the PTF in both space and time (Allen and Loneragan 2010; Jaiteh et al. 2013). Dolphin bycatch events are spread across the four Management Areas open to trawling and across all depths (50–100+ m) in the fishery. Fernández-Contreras et al. (2010) suggested that limiting trawling to deeper waters would reduce common dolphin bycatch in the pelagic trawl fishery off north-western Spain. The operators in the PTF have periodically undertaken spatial restrictions in fishing effort in response to declining stocks of target species in the past (Department of Fisheries 2013), but the results of our study suggest that such a spatial restriction within the PTF would be highly unlikely to reduce dolphin bycatch.

2.4.4 Skippers' logbook data and independent observer coverage

The extensive databases of logbook and observer records formed the basis of this assessment of spatial and temporal patterns of dolphin bycatch in the PTF, but some problems were evident in the quality of the data. Due to errors such as blank fields and erroneous location data in the logbook dataset, only ca. 90% of the trawl records could be analysed. More blank fields and errors were seen in the observer data, particularly from 2004 to 2006, and only ca. 85% of these records were of sufficient

quality for analyses. Sound reporting practices and validation checks would improve the quality of these data sources and their value for interpreting patterns of bycatch.

The dolphin bycatch rates from the independent observer coverage data were more than double those reported in the skippers' logbooks. The under reporting of bycatch by skippers is not unusual (e.g., Read et al. 2006; Moore et al. 2010), but highlights the importance of having enough observer coverage to provide robust estimates of dolphin bycatch and other incidental catches in non-selective fisheries. The Department of Fisheries specified that minimum observer coverage of 22% of total fishing effort was required from 2006-2007 onward (Stephenson et al. 2006), but the 2003–2009 data indicated that overall coverage was ca. 16% and declined over time from 17% in 2006–2007 to 8% in late 2009, when it ceased. This low and declining coverage, combined with the relatively infrequent incidence of dolphin capture, means that estimates of dolphin bycatch rates are imprecise and that the comparisons of dolphin bycatch rates between the different net designs have low power.

The amount of observer coverage required (to give 20% CV) was calculated, in this study, at between 30% and 62% of total fishing effort. Due to the high financial cost of independent observer programs, an electronic observer system involving deck-mounted video cameras was trialled in the PTF as an alternative to human observers (Diver 2012). The evaluation of this system concluded that it should not be used to replace independent observers, because of: the technical difficulties associated with maintaining the system in such a remote fishery; the system's lack of capability in differentiating between species of both targeted catch and incidental bycatch; the system's inability to detect dolphins that are caught and then fall from the BRD's

escape hatch prior to being landed on deck; and the fact that the system is only of moderately lower cost than human observers when compared over a five-year period with observer coverage rates of ca. 60% or more (Diver 2012). The cost advantage of an electronic observer system should also be considered against the human observer's better reliability (far lower chance of data loss), ability to collect more detailed and accurate data on both target and non-target catch and capability to perform other tasks (such as otolith collection) for research and management purposes (Diver 2012). The independent observer program has not recommenced since its cessation in September 2009 and the Department of Fisheries adopted an electronic observer system for further trials in the PTF in 2012. Thus, more recent comparisons of the dolphin bycatch rates reported by skippers and independent observers cannot be made.

2.4.5 Acoustic pingers as an alternative strategy for mitigating dolphin bycatch

Acoustic alarms or deterrents, ''pingers'', were designed to alert marine mammals to the presence of fishing gear and/or deter them from approaching fishing gear and aquaculture operations. They are often deployed in static fisheries, such as gill nets and long lines. The Department of Fisheries conducted trials of trawl nets equipped with active and inactive pingers and monitored by underwater video cameras in the PTF, yielding no differences in the number of dolphins swimming into the nets (Stephenson and Wells 2006). Pinger trials were subsequently abandoned in favour of the compulsory introduction of BRDs across the fishery (Stephenson et al. 2006). The Department of Fisheries later (2012) conducted another trial of larger, louder pingers in the PTF (Department of Fisheries 2013), but results were not reported. Pingers have been shown to reduce the bycatch of some cetaceans, including harbor porpoises (*P. phocoena*), Franciscana dolphins (*Pontoporia blainvillei*) and common dolphins

(reviewed in Dawson et al. 2013). However, they do not elicit consistent responses in all small cetacean species, nor do they have the same effects across all types of fisheries. For example: gill nets equipped with active pingers induced only subtle behavioural changes, rather than an avoidance response, in bottlenose dolphins (Cox et al. 2003); a more recent study found fewer bottlenose dolphins approaching within 100 m of pinger-equipped gill nets, suggesting that pingers reduce the frequency of, but do not eliminate, interactions (Waples et al. 2013); and Berg Soto et al. (2013) found that pingers elicited only subtle behavioural responses in Australian snubfin and humpback dolphins, suggesting they may not be effective in reducing bycatch of these species in gill nets or anti-shark meshing for bather protection and that alternative mitigation measures should be explored.

Pingers deployed in a pelagic pair trawl fishery did not reduce common dolphin bycatch (Northridge et al. 2003), although more recent trials of louder pingers showed promise (Northridge et al. 2011). The sample sizes used in the recent trials were, however, too small to provide statistically robust evidence of their efficacy (Northridge et al. 2011). Entanglements of bottlenose dolphins in various pinger-equipped fishing nets suggest that they are not an effective means of bycatch mitigation for this species (Dawson et al. 2013). The dolphins interacting with the PTF exhibit a number of attributes that suggest that pingers are unlikely to deter them from interacting with the trawl nets or to reduce dolphin bycatch: for example, bottlenose dolphins are known to be behaviourally flexible; they are not only aware of the presence of trawl fishing gear, but highly motivated by foraging and socializing opportunities to interact with the gear; and, they appear to show fidelity to the region and foraging around trawlers (Allen and Loneragan 2010; Jaiteh et al. 2013).

2.4.6 Conclusions and recommendations

i. An estimated minimum of ca. 500 bottlenose dolphins was incidentally caught in the Pilbara Trawl Fishery in the decade 2003-2012;

ii. Spatial and/or temporal fisheries management adjustments to fishing effort are unlikely to be effective in significantly reducing dolphin bycatch, as the extent of interactions between the dolphins and the PTF are great, the motivations for the dolphins to interact with the PTF and undertake risky behaviour are considerable and bottlenose dolphins are behaviourally adaptable;

iii. Pingers are unlikely to be effective in reducing interactions between bottlenose dolphins and the PTF, due to the active and already-noisy nature of trawl fisheries (i.e., dolphins are aware of the presence of the fishing gear irrespective of pingers), as well as the reasons listed above regarding dolphin behaviour;

iv. There has been no further reduction in dolphin bycatch since the BRDs were introduced, with an unknown quantity of bycatch falling out of bottom-opening escape hatches and, thus, not being reported;

v. Modified BRDs, with top-opening escape hatches, may be a more effective means of reducing dolphin bycatch;

vi. Extensive independent observer coverage, as well as in-net video collection, are essential in order to quantify bycatch and estimate any reductions in bycatch with greater precision and statistical power following modifications to BRDs;

vii. The effectiveness of modified BRDs should be assessed in future, and the acceptable levels of human-caused dolphin mortality in the PTF should be calculated.

Chapter Three: Genetic isolation between coastal and offshore, fishery-impacted bottlenose dolphin (*Tursiops* spp.) populations of north-western Australia

3.0 Abstract

The species affiliations and genetic connectivity of bottlenose dolphin (*Tursiops* spp.) populations off remote north-western Australia were evaluated in this study. Particular focus was placed on pelagic "offshore" dolphins subject to bycatch in a trawl fishery. A total of 71 dolphins biopsied beyond the 50 m depth contour and up to 170 km offshore, including bycaught and free-ranging individuals, were analysed; as well as 273 dolphins sampled at 12 coastal sites between the coast and the 20 m depth contour, within 10 km of the coast. Results from 19 nuclear microsatellite markers showed significant population structure between the trawler-associated and coastal dolphins, but also among coastal sites, identifying three coastal genetic clusters. A Bayesian framework and a quantitative model-testing approach found no gene flow or recruitment into the trawler-associated population from coastal populations. Mitochondrial DNA corroborated these findings of reproductive isolation between the trawler-associated population and all coastal populations. Most trawler-associated individuals formed a monophyletic clade with common bottlenose dolphins (*T. truncatus*), while all 273 "coastal" individuals formed a well-supported clade of Indo-Pacific bottlenose dolphins (*T. aduncus*). These results better define the population boundaries of the pelagic *T. truncatus* and represent an important step toward informing protected species conservation and management. Future research should focus on estimating dolphin population size (Chapter 4) and, thus, determining the impact of ongoing fishery-caused mortalities on the *T. truncatus* population.

3.1 Introduction

Estimating population parameters, such as effective population size (N_e), migration rate (m) and its directionality, as well as the degree of admixture, are important in both evolutionary biology and conservation (Waples and Gaggiotti 2006). Whether individuals form part of a single, randomly mating population or are members of different populations with varying levels of genetic isolation can have important bearings on how to manage anthropogenic impacts on wildlife (Frankham et al. 2010). Genetic data are frequently employed to determine if, and to what extent, samples from different sites are part of the same population or whether they are genetically differentiated, because information on geographic separation is not usually sufficient to determine the degree of isolation (Beerli and Palczewski 2010).

Genetic differentiation between populations may be observed in cases where there has been an historic cessation of gene flow, or where there is increased genetic drift owing to ongoing, but only low, levels of gene flow (Nielsen and Wakeley 2001; Palsbøll et al. 2004). Discriminating between these two scenarios has important ramifications for conservation, as isolated populations impacted by anthropogenic stressors may require different management strategies from those that are connected to others by the homogenizing effects of gene flow. Common management goals, such as maintaining populations, genetic diversity and the sustainable removal of individuals, are predominantly linked to evolutionary criteria of populations (Reiss et al. 2009). Achieving such goals can be challenging in the marine environment, particularly given the apparent lack of obvious boundaries between populations (e.g., Bilgmann et al. 2014).

The incidental capture, or bycatch, of cetaceans in fisheries is a long-standing and persistent anthropogenic threat to many populations around the globe (DeMaster et al. 2001; Reeves et al. 2013), with gill netting, purse seining and trawling operations resulting in the greatest proportions of fisheries-related mortalities (Northridge and Hofman 1999; Read et al. 2006; Hamer et al. 2008; Slooten 2013). The extremely variable nature of cetacean-fisheries interactions requires approaches to bycatch mitigation that are specific to cetacean species and fishery type (Bache 2003; Cox et al. 2004, 2007). The species designation of the dolphins interacting with the Pilbara Trawl Fishery (PTF hereafter) was unknown, but assumed to be the common bottlenose dolphin (*Tursiops truncatus*), about which very little is known in Australian waters (Bannister et al. 1996; Ross 2006; Allen et al. 2012; Woinarski et al. 2014). Both common bottlenose dolphins (*T. truncatus*) and Indo-Pacific bottlenose dolphins (*T. aduncus*) interact with prawn- and fish-trawling operations wherever they occur around Australia (e.g., Hill and Wassenberg 1990; Chilvers and Corkeron 2001; Svane 2005), including the waters of the remote north-western Australian coastline (Jaiteh et al. 2013; Allen et al. 2014).

Correct species identification is a critical component in wildlife conservation, since different species possess different behavioural and life history characteristics (Wade and Angliss 1997; Boness et al. 2002). Furthermore, knowledge of genetic structure and gene flow provide a means of assessing connectivity of populations, which can inform scientists and decision-makers about the impacted population's ability to withstand, or recover from, anthropogenic sources of mortality (Hoelzel et al. 1998b; Pichler et al. 1998; Palsbøll et al. 2007; Wade et al. 2012).

Bottlenose dolphins are polytypic, with two species recognised based on both genetics and morphology; *T. truncatus* and *T. aduncus* (Rice 1998; Wang et al. 1999; Wang et al. 2000a, b), and a third proposed recently; *T. australis* (Möller et al. 2008; Charlton-Robb et al. 2011). The number of species in the complex, however, remains to be resolved (Natoli et al. 2004), with the Society for Marine Mammalogy currently recognising only *T. truncatus* and *T. aduncus* (Committee on Taxonomy 2014). All three putative species are present in Australian waters, with *T. truncatus* and *T. aduncus* having wide distributions (Hale et al. 2000; Kemper 2004; Möller and Beheregaray 2001). *Tursiops truncatus* are thought to occur further offshore and in deeper waters than *T. aduncus* (Ross 2006; Woinarski et al. 2014).

The use of the mitochondrial control region for phylogenetic species identification has proven effective in a range of other studies for closely related delphinids (Rosel et al. 1994; Möller and Beheregaray 2001; Ross et al. 2003; Beasley et al. 2005). This marker system also has limitations, however, and its usefulness for species identification depends on the evolutionary distinctiveness of the taxa in question. In studies attempting to elucidate the evolutionary relationships amongst the Delphininae, the use of a single mitochondrial gene has provided limited resolution, due to high levels of intraspecific variation and low interspecific differences. Kingston et al. (2009) found that data from amplified fragment length polymorphisms (AFLPs), representing many nuclear genes, gave better resolution. However, even use of genome-wide multi-locus datasets such as this, and others (Xiong et al. 2009; McGowen 2011; Zhou et al. 2011), have been unable to resolve relationships unambiguously within this group, which is thought to have undergone a recent and rapid radiation (Kingston et al. 2009; Vilstrup et al. 2011; Hassanin et al. 2012).

The genetic relationships of the genus *Tursiops* itself remains enigmatic, with many studies finding that it is polyphyletic (Kingston et al. 2009; Xiong et al. 2009; Vilstrup et al. 2011; Zhou et al. 2011; Hassanin et al. 2012; but see McGowen 2011). Regardless of their relationships to each other, the *Tursiops* species themselves resolve as monophyletic clades and are genetically distinct (Xiong et al. 2009). For example, using complete taxon sampling within the Delphininae and multiple individuals for each taxon, *T. truncatus* and *T. aduncus* both sorted as monophyletic clades in a mtDNA control region tree (Kingston et al. 2009). Although lacking strong bootstrap support (*T. truncatus* < 50%, *T. aduncus* = 68%), their monophyletic nature makes them suitable for species identification when unknowns fall within these groups (Kingston et al. 2009).

Coastal bottlenose dolphins of north-western Australia were formerly assigned to *T. aduncus* based on visual assessments alone (Allen et al. 2012). *Tursiops aduncus* are subject to in-depth research in most Australian states (e.g., Chilvers and Corkeron 2003; Wiszniewski et al. 2010; Randić et al. 2012; Kemper et al. 2014). Prior to this study, however, no detailed data have been published on any population of this species north of Shark Bay in Western Australia, other than confirmation of their occurrence adjacent to urban centres (Allen et al. 2012). This lack of information is surprising in view of the frequency of Environmental Impact Assessments having been carried out in order to gain approvals for hydrocarbon and mineral extraction across the region (Bejder et al. 2012).

In this study, the demography and species status of a number of putative populations of dolphins off north-western Australia were investigated. Tissue samples (biopsies) were collected from incidentally captured and free-ranging dolphins interacting with the PTF (> 50 m depth), as well as from dolphins in deeper waters (> 100 m) off the North West Cape, and at multiple shallow (≤ 20 m) coastal sites inshore of the fishery and across north-western Australia. The primary aim of this research was to determine whether dolphins from the PTF showed greater genetic affinities to the common bottlenose dolphin, the Indo-Pacific bottlenose dolphin, or other closely related delphinid taxa. In addition to the traditionally used combination of basic genetic summary statistics and population structure analyses, model-based coalescent analyses of genetic connectedness between dolphin populations across the region were completed. This approach aimed to elucidate whether or not dolphins recruited into the PTF-associated population from nearby sites. This study represents the first assessment of the genetic identity and structure of north-western Australian bottlenose dolphins and provides important information upon which to base future decisions on fisheries and population management.

3.2 Materials and Methods

3.2.1 Pilbara Trawl Fishery and coastal sampling sites

Biopsy sampling efforts were focussed at 15 sites around north-western Australia (Fig. 3.1, Table 3.1). The PTF extends from 116ºE to 120ºE and an area of 23,000 km^2 is open to trawl fishing. Further details on the characteristics of the PTF are provided in Chapter 2 and Allen et al. (2014).

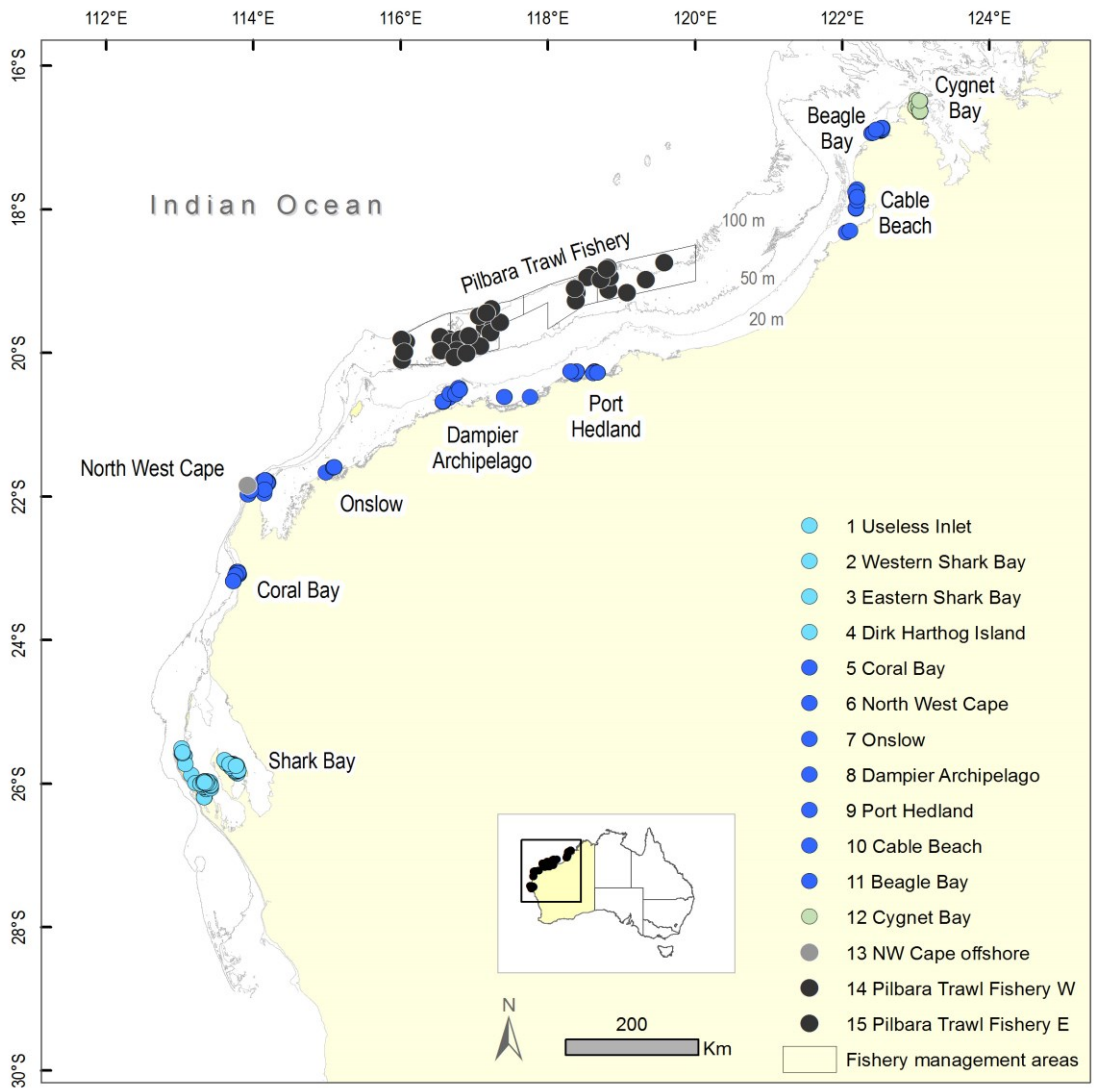

Figure 3.1. Map of the sampling sites, north-western Australia, showing the biopsy sample collection sites for: incidentally captured and free-ranging dolphins associating with the Pilbara Trawl Fishery (n=68); dolphins in deep water off the North West Cape (n=3); and shallow water, coastal dolphins (n=273) from 12 sites. The boundaries of the PTF fisheries management areas and the 20 m, 50 m and 100 m depth contours are also shown.

All dolphin biopsy samples from within the fishery were collected between ≈ 50 and 170 km offshore, in water > 50 m deep, and over an east-west distance of ≈ 300 km. An eastern and a western cluster of samples were collected in the PTF; Site 15 samples, the PTF East, were collected around 119°E, while Site 14 samples, the PTF West, were collected ≈ 160 km to the west, between 116°E and 117°E. Another three

samples were collected ≈ 300 km to the south-west of the PTF: in deep water offshore of the North West Cape (Site 13, NW Cape offshore, 114°E, Fig. 3.1, Table 3.1). These three samples were included in this study to provide insight, albeit limited by the small sample size, into genetic connectedness of the PTF-associated dolphins to other 'offshore' populations. Coastal bottlenose dolphins were sampled at 12 sites in waters ≤ 20 m deep and within about 10 km of the coastline (Fig. 3.1, Table 3.1). These sites extended from Useless Inlet (Site 1, 26.1°S, 113.3°E) in Shark Bay in the south-west to Cygnet Bay (Site 12, 16.5°S, 123.0°E) in King Sound in the north-east (Fig. 3.1, Table 3.1).

Table 3.1. Summary of the regions, sampling sites and depth ranges at which dolphins were biopsy sampled across north-western Australia. Blue = shallow/coastal sites; Black = deep/offshore sites. N = number of biopsy samples collected. PTF = Pilbara Trawl Fishery.

Region, site number and name	Latitude, Longitude	Depth range (m)	N
Shark Bay			
1. Useless Inlet	26.1°S, 113.3°E	2-8	33
2. Western Shark Bay	26.0°S, 113.4°E	1-16	21
3. Eastern Shark Bay	25.7°S, 113.7°E	2-15	53
4. Dirk Hartog Island	25.5°S, 113.1°E	4-17	16
Other Coastal			
5. Coral Bay	23.1°S, 113.8°E	5-18	14
6. North West Cape	21.8°S, 114.1°E	2-20	26
7. Onslow	21.6°S, 115.1°E	5-13	6
8. Dampier Archipelago	20.6°S, 116.7°E	6-13	27
9. Port Hedland	20.3°S, 118.6°E	5-12	25
10. Cable Beach	18.0°S, 122.2°E	3-20	17
11. Beagle Bay	16.8°S, 122.6°E	3-15	15
12. Cygnet Bay	16.5°S, 123.0°E	3-17	20
13. NW Cape offshore	21.8°S, 114.0°E	101	3
Pilbara Trawl Fishery			
14. PTF West	19.8°S, 116.8°E	54-101	47
15. PTF East	18.8°S, 119.0°E	73-103	21

3.2.2 Sample collection and generation of genetic data

A total of 344 dolphin biopsy samples were collected between 2008 and 2013 (except those from Shark Bay, which were obtained between 1998 and 2013) and used for genetic analyses in this study. The subset of 68 samples of PTF-associated dolphins included three from incidentally caught dolphins and 65 collected from free-ranging dolphins during commercial fish trawling operations on trips to sea in October-November 2008, March-April 2009, and April 2011. Biopsies were obtained from free-ranging dolphins within the PTF using the PAXARMS remote biopsy system (Krützen et al. 2002) from a small (4.5 m) tender, and a biopsy pole for sampling dolphins close to the bow or stern of vessels (Bilgmann et al. 2007) from a trawler. All 273 bottlenose dolphins sampled from the 12 coastal sites were collected using the remote biopsy system from a small (< 6 m) research vessel.

DNA was extracted from the biopsy samples using the Qiagen Gentra tissue kit following the manufacturer's instructions. The extracted genomic DNA was re-suspended in TE buffer (10mM Tris, 1mM EDTA, pH 8) and the concentration adjusted to 20 ng/µl. Sex determination was carried out by amplification of the sex specific ZFX and SRY loci using a multiplex PCR (Gilson et al. 1998).

Part of the hyper-variable region I of the mitochondrial control region (HVR-I) was amplified using primers dlp1.5 and dlp5 (Baker et al. 1993). PCR products were cleaned up using silica membrane spin columns (GeneElute^{TM} by Sigma-Aldrich) and sequenced using the Cycle Sequencing Ready Reaction kit (Applied Biosystems), based on the protocol described in Bacher et al. (2010). SEQUENCING ANALYSIS v5.2 and BIOEDIT v7.0.5.3 were used to quality control, edit and align the sequences.

Nineteen microsatellite loci were amplified using two different multiplex PCR regimes: 1 - Tur4_98, Tur4_117, MK6, E12, Tur4_105, Tur4_108, Tur4_66, Tur4_111, Tur4_128; 2 - KWM12, MK3, MK5, MK8, MK9, Tur4_142, Tur4_153, Tur4_162, Tur4_80, Tur4_132 (Krützen et al. 2001; Hoelzel et al. 1998a; Nater et al. 2009). Diluted PCR products were denaturised in 10 µl HiDi formamide containing 0.07 µl of GeneScanTM500LIZ size standard (Applied Biosystems). The length of the DNA fragments were analysed on an ABI 3730 DNA Sequencer (Applied Biosystems) using GENEMAPPER v4.0.

3.2.3 Population structure and gene flow

Population structure and genetic connectedness between sampling localities were inferred using both summary statistics and individual-based approaches based on microsatellite data. Genetic variation within sampling sites was estimated by calculating the number of alleles and effective alleles, observed (H_O), expected (H_E) and unbiased expected heterozygosity (UH_E) in GENALEX v6.5 (Peakall and Smouse 2012). Departure from Hardy-Weinberg equilibrium (HWE) and tests for linkage disequilibrium were carried out in GENEPOP v4.2.1 (Rousset 2008), with Bonferroni-corrected significance levels (Rice 1989). Estimates of F_{ST} (Weir and Cockerham 1984) and Jost's D (Jost 2008), measures of population differentiation due to genetic structure, were calculated in GENEPOP and GENODIVE (Meirmans and van Tienderen 2004), respectively.

The software package STRUCTURE v2.3.3 (Pritchard et al. 2000) was used to determine the number of genetic clusters in the dataset, particularly the levels of genetic connectedness between the PTF-associated population/s and the 12 coastal

dolphin sampling localities. The STRUCTURE algorithm allocates sampled individuals into a number of clusters (*K*) independent of locality information by minimizing deviations from Hardy-Weinberg and linkage equilibrium in each cluster. The program uses a Markov Chain Monte Carlo (MCMC) procedure to estimate P(X|*K*), the posterior probability that the data fit the hypothesis of *K* clusters.

Three different STRUCTURE analyses were conducted. For all analyses, the length of the burn-in period was set to 10^5, followed by 10^6 MCMC steps. For each *K*, the analysis was run ten times. The first ('global') analysis involved all samples and used an admixture model with correlated allele frequencies and no prior information. For the two subsequent analyses, the Locprior model was chosen, which improves clustering when the signal is weak without spuriously inferring structure, if absent (Hubisz et al. 2009). The second analysis was carried out on PTF individuals only, while the third analysis only incorporated the 12 coastal populations. Since the P(X|K) estimator has been shown to overestimate *K*, as it frequently plateaus at higher values than biologically meaningful estimates of *K*, the Δ*K* statistic was also calculated (Evanno et al. 2005). This provides a conservative estimate of *K* and was performed using the software STRUCTUREHARVESTER (Earl and vonHoldt 2012).

In addition, a factorial correspondence analysis projecting all genotypes on the factor space, which is defined by the similarity of their allelic states (as implemented in GENETIX v4.05.2 - Belkhir et al. 2004), was used to visualise the degree of dissimilarity between sampling sites. Factorial correspondence analysis is similar to principal components analysis, providing a means of summarising data in a two-dimensional graphical form, but it employs categorical rather than continuous data.

Migration patterns and gene flow between the PTF population and (some of) the coastal populations were inferred based on the coalescence approach implemented in MIGRATE-N v3.2 (Beerli and Felsenstein 2001; Beerli 2006). In order to reduce the number of parameters in the models to arrive at a computationally and statistically tractable analysis, some relevant sampling sites were pooled into three populations (as identified in our STRUCTURE analysis, see Results): Pilbara Trawl Fishery (PTF, Sites 14-15), Shark Bay (Sites 1-4), and Coastal (Sites 5-11) (Fig. 3.1, Table 3.1). Four different models constraining the presence, directionality, and amount of gene flow among the three pooled sampling sites were defined. Model 1 allowed full migration between all population pairs ('full' model). A model that sets migration between PTF and all other populations to 0 could not be used because, under such circumstances, coalescence trees could not be calculated and general assumptions of the MIGRATE-N approach were violated. Therefore, model 2 allowed only very limited gene flow to and from the PTF (close enough to zero migration, but sufficient to match MIGRATE-N's needs with regard to coalescence trees). This effectively rendered the PTF population isolated from both Shark Bay and Coastal populations, while it allowed full migration between Shark Bay and Coastal ('low migration PTF' model). In model 3, the PTF constituted a source for Shark Bay and Coastal, but did not receive migrants from the latter two populations ('PTF source' model). In model 4, the PTF received migrants from Shark Bay and Coastal, but there was no migration in the other direction ('PTF sink' model) (Table 3.3). The software MIGRATE-N was also used to calculate Bezier approximation scores (BAS) to identify the best-fitting model.

The run parameters were as follows: for Θ (population size parameter, scaled to mutation rate) and M (migration rate parameter), a uniform prior was used. The prior range for Θ was set to 0-10 (mean 5; Δ 1; 20,000 bins) and for M 0-100 (mean 50; Δ 10; 20,000 bins). Mutation rates of loci were allowed to vary. Initial runs showed problems of parameter divergence. Runtime was therefore increased considerably and 50 replicate analyses were used, from which the posterior distributions could be drawn with much better confidence (e.g., Hartmann et al. 2013). Five hundred steps were recorded per replicate every 100 iterations, thus sampling 25,000 parameter values from chains comprising 2,500,000 steps. A static heating scheme (4 chains with temperatures 1,000,000; 3; 1.5; 1) and a burn-in of 200,000 steps was applied to each replicate. Model comparisons were carried out using marginal likelihoods calculated using the thermodynamic integration in MIGRATE-N (Beerli and Palczewski 2010). The estimated mutation scaled migration parameter *M* was translated into the effective number of immigrants per generation (*Nm*) as detailed in Kraus et al. (2013) and Jonker et al. (2013).

To obtain estimates of the magnitude and direction of contemporary gene flow between pairs of populations, the software BAYESASS v3.0.3 was used (Wilson and Rannala 2003). The advantage of this approach is that, without assuming genetic equilibrium, it uses a MCMC algorithm to estimate the posterior probability distribution of the proportion of migrants (M) between pairs of populations. The same four population classifications as for the MIGRATE-N analysis were used, conducting five independent runs for 10,000,000 generations, discarding the first 1,000,000 generations as burn-in. Mixing parameters for migration rates (m), allele frequencies (a), and inbreeding coefficient (f) were 0.3, 0.5, and 0.5, respectively.

3.2.4 Phylogenetic analyses

The mitochondrial DNA (mtDNA) sequence alignment was trimmed to the shortest sequence (426bp) and identical haplotypes were collapsed using DAMBE v5.0.72 (Xia and Xie 2001). As a mutation model, a General Time Reversible Model with gamma-distributed rate variation across sites and a proportion of invariable sites was used, as implemented in MRBAYES v3.2. Parameters for the MRBAYES run were four heated chains running for 10,000,000 generations, with a sampling frequency of 1,000 and a burn in of 2,500 data points. Consensus trees were displayed and printed using FIGTREE v1.1.2 (http://tree.bio.ed.ac.uk/).

To assess the phylogenetic affiliations of the PTF-associated and coastal bottlenose dolphins with other delphinids, previously published HVR-I sequences from the following species and regions were included in the analysis: common (*T. truncatus*) and Indo-Pacific (*T. aduncus*) bottlenose dolphins, principally from Chinese and Indonesian waters (Wang et al. 1999), as well as the recently delineated Burrunan dolphin from Southern Australia (*T. australis*; Charlton-Robb et al. 2011) and Fraser's dolphin (*Lagenodelphis hosei*; Caballero et al. 2008) (Appendix 3.1).

Tursiops aduncus samples from coastal south-eastern Australia were also included (Möller and Beheregaray 2001; Möller et al. 2008; Wiszniewski et al. 2010). The tree was rooted with an Atlantic white-sided dolphin (*Lagenorhynchus acutus*; Cipriano 1997) sequence as an outgroup (Appendix 3.1).

3.3 Results

All 19 microsatellite loci were in Hardy-Weinberg equilibrium and no significant linkage disequilibrium was observed. The allelic diversity and heterozygosity values were generally higher for the PTF samples than the coastal sampling sites (Appendix 3.2).

The pairwise F_{ST} values were small (generally < 0.06), but significant between almost all sampling sites (Table 3.2). The highest values (generally > 0.20) were observed for all pairwise comparisons between offshore and coastal sampling sites (Table 3.2). This suggests a longer period of isolation between offshore and coastal populations than between different coastal sampling sites. Pairwise values for Jost's D were generally larger than F_{ST} values. In particular, pairwise comparisons between PTF and coastal populations were generally two to three times larger for Jost's D than for F_{ST}, suggesting that F_{ST} underestimates divergence (Whitlock 2011).

For the global dataset containing all samples, the Evanno method identified that K=2 clusters was the most likely scenario. The STRUCTURE analysis illustrated a clear pattern of genetic differentiation between the offshore (both the PTF and NW Cape offshore) and all coastal sampling sites at all levels of K>1 (Fig. 3.2A). For higher K values for the global data set, visual inspection revealed four distinct clusters: (*i*) the four Shark Bay coastal sites; (*ii*) all coastal sites from Coral Bay to Beagle Bay; (*iii*) coastal Cygnet Bay; and (*iv*) the NW Cape offshore and PTF (Fig. 3.2A).

Table 3.2. Pairwise F_{ST} (above) and Jost's D (below the diagonal) values between sampling sites. Significant F_{ST} values are given in bold. The shaded area represents offshore-coastal population comparisons. Site numbers as per Fig. 3.1, Table 3.1 and left column.

Sampling Site	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
1 Useless Inlet		0.006	**0.031**	**0.038**	**0.059**	**0.042**	**0.025**	**0.041**	**0.033**	**0.060**	**0.046**	**0.065**	**0.251**	**0.279**	**0.263**
2 Western Shark Bay	0.025		**0.028**	**0.018**	**0.045**	**0.032**	**0.018**	**0.043**	**0.039**	**0.060**	**0.047**	**0.059**	**0.234**	**0.272**	**0.254**
3 Eastern Shark Bay	0.106	0.003		**0.036**	**0.054**	**0.066**	**0.044**	**0.053**	**0.039**	**0.060**	**0.058**	**0.082**	**0.259**	**0.279**	**0.263**
4 Dirk Hartog Island	0.225	0.041	0.004		**0.047**	**0.052**	**0.033**	**0.042**	**0.038**	**0.067**	**0.036**	**0.062**	**0.230**	**0.263**	**0.243**
5 Coral Bay	0.123	0.145	0.173	0.186		**0.015**	0.008	**0.020**	**0.025**	**0.028**	0.005	**0.051**	**0.233**	**0.264**	**0.244**
6 North West Cape	0.117	0.009	0.016	0.003	0.040		0.009	**0.020**	**0.032**	**0.040**	**0.022**	**0.067**	**0.285**	**0.291**	**0.276**
7 Onslow	-0.097	-0.126	-0.085	-0.004	0.076	-0.038		-0.006	0.017	0.006	0.009	**0.040**	**0.192**	**0.252**	**0.230**
8 Dampier Archipelago	0.104	0.001	-0.002	-0.004	0.063	-0.026	-0.097		**0.008**	0.010	**0.012**	**0.051**	**0.231**	**0.268**	**0.249**
9 Port Hedland	0.081	0.088	0.130	0.149	-0.059	0.023	0.001	0.032		**0.028**	**0.012**	**0.044**	**0.238**	**0.264**	**0.248**
10 Cable Beach	-0.016	0.101	0.107	0.253	0.178	0.175	-0.105	0.124	0.142		**0.036**	**0.057**	**0.199**	**0.253**	**0.233**
11 Beagle Bay	0.145	0.107	0.168	0.151	-0.051	0.021	0.093	0.062	-0.037	0.264		**0.047**	**0.230**	**0.256**	**0.233**
12 Cygnet Bay	0.250	0.214	0.225	0.188	-0.038	0.067	0.193	0.105	-0.001	0.324	-0.030		**0.199**	**0.247**	**0.231**
13 NW Cape offshore	0.491	0.774	0.685	0.873	0.706	0.835	0.480	0.721	0.685	0.235	0.892	0.861		**0.070**	**0.063**
14 PTF West	0.473	0.686	0.643	0.791	0.613	0.721	0.492	0.664	0.609	0.319	0.743	0.735	0.157		0.002
15 PTF East	0.418	0.626	0.574	0.721	0.563	0.661	0.396	0.589	0.551	0.246	0.701	0.692	0.092	-0.041	

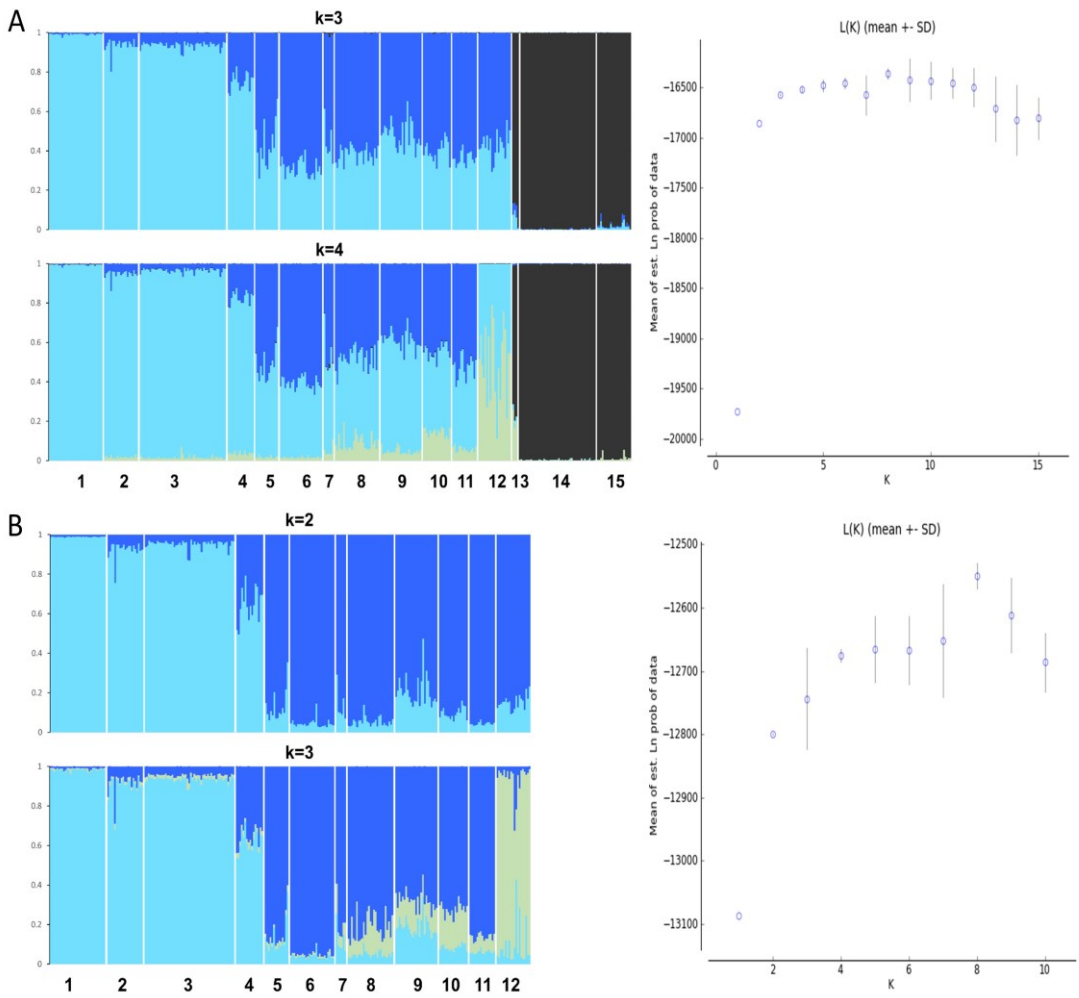

Figure 3.2. STRUCTURE plots (each column representing an individual dolphin, with sampling sites separated by a white line) and log-likelihoods for different number of clusters, *K*: A. Full dataset including all north-western Australian samples (n = 344). B. Coastal samples only (n = 273). The sampling site numbers correspond to their geographical site from the south-west to the north-east (coastal and then offshore) as in Fig. 3.1 and Table 3.1: 1 Useless Inlet; 2 Western Shark Bay; 3 Eastern Shark Bay; 4 Dirk Hartog Island; 5 Coral Bay; 6 North West Cape; 7 Onslow; 8 Dampier Archipelago; 9 Port Hedland; 10 Cable Beach; 11 Beagle Bay; 12 Cygnet Bay; 13 NW Cape offshore; 14 PTF West; 15 PTF East.

When only PTF samples were considered, *K*=1 had the highest probability, suggesting no genetic sub-structuring within the PTF. When coastal samples only were considered (Fig. 3.2B), Shark Bay sites formed a distinct cluster from all other coastal sites. At *K*=3 and higher, samples from Cygnet Bay became distinct, while the remaining coastal populations continued to form one cluster. There was also a peak at *K*=8. However, given the relatively

small number of genetic markers and the large number of sampling locations, as well as the focus on fishery-impacted dolphins, scenarios with higher *K*s should await analyses with a larger number of markers.

The factorial correspondence analysis based on 19 microsatellite loci (Fig. 3.3) strongly supported the STRUCTURE results. Samples from the PTF formed a single distinct cluster compared to all other samples, including North West Cape offshore. Among the coastal sites, the four Shark Bay sites in the south-west were clearly distinct from other coastal sites, while Cygnet Bay was distinct in the north-east. All other coastal sites could not be distinguished from each other (Fig. 3.3).

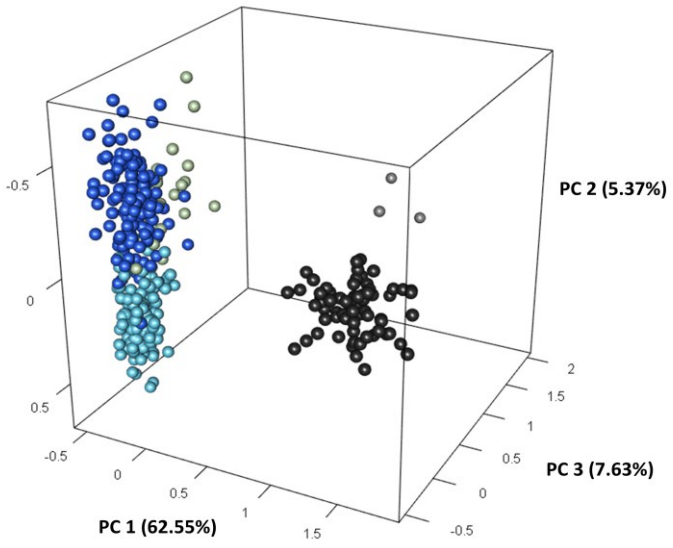

Figure 3.3. Three-dimensional representation of a factorial correspondence analysis projecting all sampled individuals of north-western Australian bottlenose (*Tursiops* spp.) dolphins on the factor space. The factor space is defined by the similarity of allelic states, in order to visualise the degree of dissimilarity between the sampling sites (Table 3.1, Fig. 3.1). The % values on the axes labels represent % variation explained, as in principal components analyses. Light blue fill = individuals sampled in coastal Shark Bay (Sites 1-4); dark blue fill = individuals sampled in coastal north-western Australia (Sites 5-11); green fill = individuals sampled in coastal Cygnet Bay (Site 12); grey fill = individuals sampled in deep water offshore of the NW Cape (Site 13); black fill = individuals sampled in the PTF (Sites 14-15).

Based on the STRUCTURE results, most sampling localities were pooled into three 'populations' to analyse migration patterns between the combination of: (*i*) all four Shark Bay coastal sites (Shark Bay); (*ii*) all other coastal sites, other than Cygnet Bay (Coastal); and (*iii*) PTF West and East into a single population (PTF). The model comparisons showed a clear lack of migration into the PTF population from any of the coastal populations. The model in which the PTF was treated as a source population to all others (PTF source), with no recruitment from coastal populations, gained highest support (Table 3.3). The second best model was also one that restricted migration into the PTF from the other two coastal populations (Low migration PTF). The likelihood differences between all models were so large as to support the best model with a probability of essentially one and dismiss the others (P. Beerli, Florida State University, pers. comm. https://groups.google.com/forum/#!topic/migrate-support/CQUkqY-wmx0). The model with the lowest support was that which allowed free migration between all populations (Table 3.3). Thus, there is a strong indication that the PTF population is reproductively isolated from coastal populations, with no recruitment of dolphins into the PTF population from nearby coastal areas.

The parameter estimates (models of Θ and *Nm* from *M*) were based on the PTF source model. As expected, Θ was highest for the pelagic PTF population (Θ = 6.37, 95% CI = 5.60-7.26). The coastal populations had smaller Θ values (Shark Bay Θ = 0.78, 95% CI 0.53-1.00; Coastal Θ = 2.90, 95% CI = 2.48-5.29). Since no gene flow from the PTF population to the two coastal populations was assumed in the best-fitting model, *Nm* estimates between the two coastal populations only are reported. *Nm* was significantly different from 0 in both cases, with *Nm* values from Shark Bay to Coastal populations being higher (SB→CO: *Nm* = 4.31, 95% CI = 3.70-7.89; CO→SB: *Nm* = 0.21, 95% CI =

0.14-0.26). Importantly, in all models, regardless of their level of support, *Nm* parameter estimates concerning migration into the PTF population were always small and confidence intervals included 0, providing further evidence of the lack of recruitment of dolphins into the PTF population from nearby coastal areas.

Table 3.3 Comparisons of different migration models. For model comparisons, sampling sites were pooled into three populations: SB = Shark Bay (Sites 1-4), CO = Coastal (Sites 5-11), PTF = Pilbara Trawl Fishery (Sites 14-15). Model parameter codes are as follows: Parameters 1-3 indicate migration into the SB populations from the SB, CO and PTF populations. Parameters 4-6 and 7-9 indicate migration into the CO and PTF populations, respectively, from the SB, CO and PTF populations. Asterisks indicate that the model estimated migration rates, 0 indicates that no migration was allowed, and c is a fixed low migration rate of 0.001.

Model	Populations and model parameters	Bezier approximation score (BAS)	ΔBAS
	SB CO PTF		
Full	*** *** ***	-359,466	133,001
Low migration PTF	**c **c cc*	-237,198	10,733
PTF source	*** *** 00*	-226,465	0
PTF sink	**0 **0 ***	-260,614	34,149

The results from the MIGRATE-N analyses were corroborated by the findings based on BAYESASS (Table 3.4). No significant migration was detected from the coastal populations into the PTF population and vice versa. In general, the proportion of detected migrants within each population (other than Cygnet Bay, where there was a large proportion, ca. 28%, of migrants from the coastal population) was extremely small and the 95% confidence intervals included 0 in almost every comparison. These findings suggest strongly that there is no, or at least extremely low, migration between the PTF, Shark Bay and Coastal populations.

Table 3.4. Mean posterior distribution values (95% confidence interval) of migrants (M) between four combined populations as determined by BAYESASS. 95% confidence intervals smaller than 0 and larger than 1 were rounded to the nearest integer.

from/to	Shark Bay	Coastal	Cygnet Bay	PTF
Shark Bay	0.982	0.013	0.003	0.003
	(0.963-1.000)	(0.000-0.031)	(0.000-0.008)	(0.000-0.008)
Coastal	0.034	0.961	0.003	0.003
	(0.000-0.071)	(0.924-0.998)	(0.000-0.007)	(0.000-0.007)
Cygnet Bay	0.022	0.284	0.681	0.013
	(0.000-0.059)	(0.235-0.334)	(0.654-0.707)	(0.000-0.037)
PTF	0.005	0.005	0.005	0.986
	(0.000-0.014)	(0.000-0.014)	(0.000-0.014)	(0.971-1.000)

The phylogenetic analyses based on mtDNA revealed some unexpected patterns. Seventeen unique haplotypes were identified among all individuals collected from within the two sampling sites in the Pilbara Trawl Fishery (Sites 14 and 15, Table 3.1, Fig. 3.1), as well as those collected in deep water offshore of the North West Cape (Site 13). These haplotypes formed a highly supported, monophyletic clade with the common bottlenose dolphin (*T. truncatus*). Within this clade, however, clear resolution was lacking (Fig. 3.4).

The haplotype of six individuals sampled within the PTF formed a highly supported, monophyletic clade (posterior probability of 0.97) with Fraser's dolphin (*Lagenodelphis hosei*) haplotypes (Fig. 3.4). While at-sea differentiation between delphinids can be difficult, all observations and photographs taken during offshore field trips were of the common bottlenose dolphin phenotype.

In contrast, all of the bottlenose dolphins sampled in the coastal regions of north-western Australia formed a highly supported monophyletic clade (posterior probability of 1.00) with other Indo-Pacific bottlenose dolphins (*T. aduncus*; Figs 3.1 and 3.4).

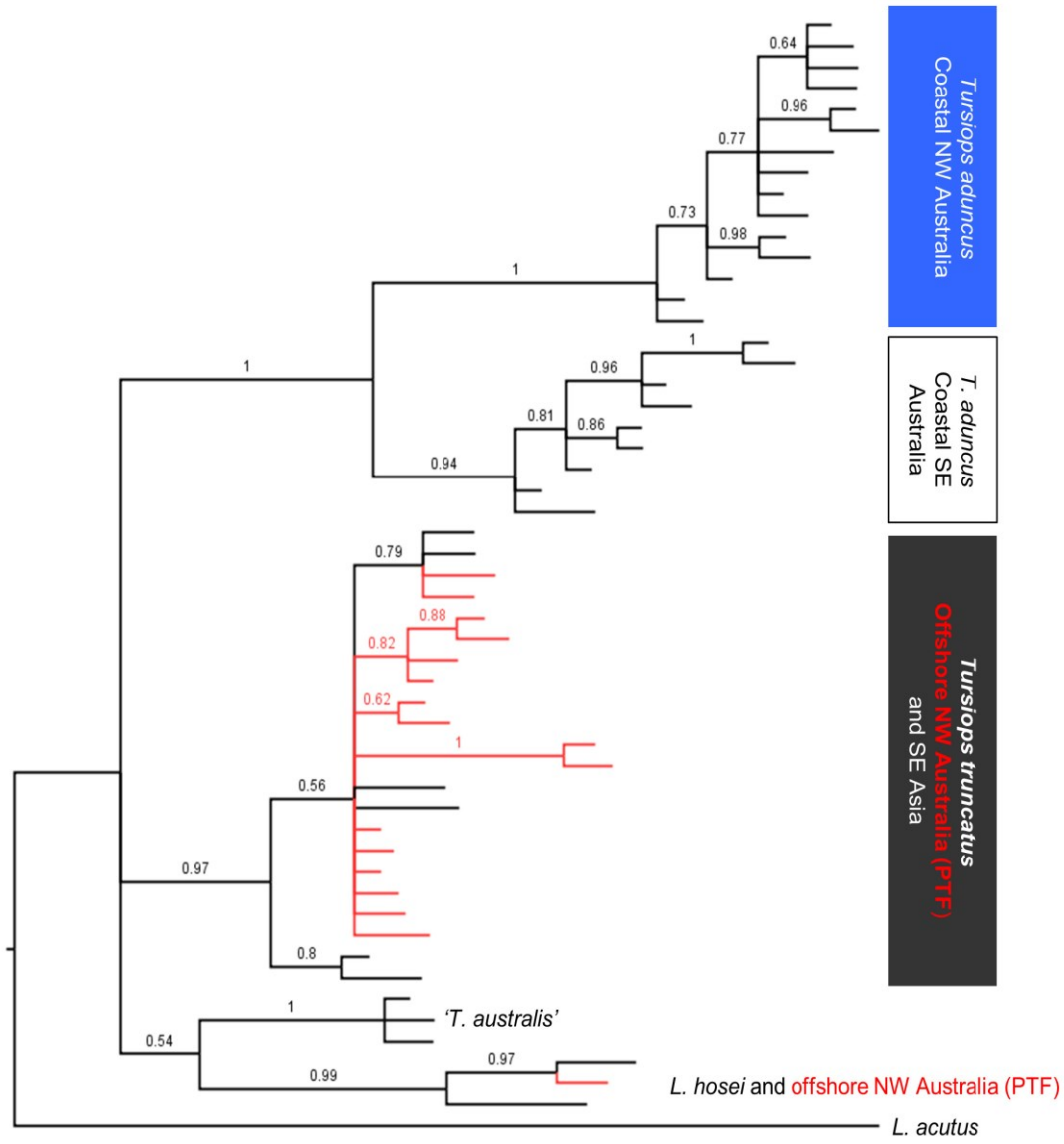

Figure 3.2. Phylogenetic relationships of offshore north-western Australian (Pilbara Trawl Fishery and North West Cape) dolphin mtDNA haplotypes (red branches) and coastal north-western Australian dolphin mtDNA haplotypes (blue block) from this study compared to relevant delphinids. Node labels are posterior probabilities.

3.4 Discussion

3.4.1 Genetic differentiation between fishery-associated and coastal dolphins

All the analyses based on nuclear microsatellite data supported the genetic differentiation between the bottlenose dolphins sampled in the offshore, pelagic environment (*Tursiops truncatus)* from those sampled coastally (*T. aduncus*). Both the STRUCTURE and factorial correspondence analyses revealed four clusters that were clearly separated geographically. Similarly strong patterns of segregation have been reported in other small cetaceans. For example, Perrin et al. (2011) used cranial osteological differentiation to support previous assertions, based on molecular data, for the existence of coastal and offshore forms of common bottlenose dolphins (*T. truncatus*) in Californian waters. Also, false killer whale (*Pseudorca crassidens*) populations sampled offshore in the central and eastern Pacific were recently differentiated from those that are resident and island-associated around the Hawai'ian Archipelago (Martien et al. 2014). The analyses in the current study did not reveal whether the genetic isolation between the Pilbara Trawl Fishery and coastal populations is due to historic cessation of gene flow (i.e., reproductive isolation followed by speciation), or increased genetic drift owing to on-going low levels of gene flow. Both the MIGRATE-N and BAYESASS analyses revealed an absence of gene-flow from any coastal population into the PTF population, strongly suggesting that the bottlenose dolphin population that is subject to bycatch in the PTF is genetically isolated from all the adjacent, coastal dolphins, and does not recruit from these coastal dolphin populations. Furthermore, no evidence of hybridisation was detected between the coastal Indo-Pacific bottlenose dolphins (*T. aduncus*) and the pelagic, common bottlenose dolphins (*T. truncatus*).

The offshore *T. truncatus* showed less genetic sub-structuring than the coastal *T. aduncus* sampled across a similar geographic distance. Furthermore, the relative effective population size of *T. truncatus* (Θ) was almost an order of magnitude larger than that of the *T. aduncus* population in Shark Bay, and more than twice as high as the combined *T. aduncus* coastal populations. These results were to be expected, given the more complex habitat features and likely environmental and social barriers to gene flow in the coastal region than further offshore (Krützen et al. 2004; Randic et al. 2012), as well as the propensity for coastal *Tursiops* of both species to adapt rapidly to local habitats (e.g., Hoelzel et al. 1998b; Sellas et al. 2005; Wiszniewski et al. 2010). Common bottlenose dolphins of open, pelagic environments are certainly capable of long-distance movements. Wells et al. (1999) documented travel distances of ca. 2,000 and > 4,000 km in < 50 days by two satellite-tracked *T. truncatus* off the East coast of the United States. Quérouil et al. (2007) found a lack of genetic differentiation between *T. truncatus* from the Azores, Madeira and other offshore areas of the north-east Atlantic, suggesting they form one large, pelagic population. The lack of baseline data on Australian *T. truncatus* means that it is not possible to assess whether the population in the PTF region is an isolated unit or forms part of a large, pelagic population (Bannister et al. 1996; Ross 2006; Woinarski et al. 2012). The relatively large Θ suggests it may be so. Comparisons of the Θ in the PTF with those of other pelagic *T. truncatus* populations in the eastern Indian Ocean and western Pacific would address this uncertainty.

3.4.2 Offshore, pelagic bottlenose dolphins of north-western Australia

Most dolphins associated with the PTF, as well those sampled in deep water off the North West Cape, exhibited haplotypes that form a monophyletic clade with those previously published for *T. truncatus* from Chinese and Indonesian waters (Wang et al. 1999). Until

this study, the Chinese and Indonesian haplotypes were the only available reference samples for *T. truncatus* in this region of the world, despite the fact that they are globally widespread, occurring from tropical to temperate waters in both coastal and pelagic populations (Rice 1998; Reeves et al. 2002).

In this study, both *T. truncatus* and *T. aduncus* formed highly supported monophyletic clades. Most individuals from within the PTF, and elsewhere offshore, fell within the *truncatus* clade, providing strong evidence that it is predominantly *T. truncatus* associating with the fishery. The complete lack of historic and contemporary gene flow between PTF *T. truncatus* and coastal *T. aduncus*, based on microsatellite data and two independent approaches to estimate gene flow, corroborated this conclusion.

Unexpectedly, some offshore individuals expressed haplotypes that share a close affinity to Fraser's dolphin haplotypes. Fraser's dolphins occur primarily in waters deeper than 1,000 m (Reeves et al. 2002). They are rarely found in shallow waters or near-shore environs, and field guides and texts report Fraser's dolphins in mixed-species assemblages with false killer, melon-headed (*Peponocephala electra*) and sperm (*Physeter macrocephalus*) whales, as well as Risso's (*Grampus grisseus*), pan-tropical spotted (*Stenella attenuata*) and striped (*S. coeruleoalba*) dolphins (Carwardine 1995; Reeves et al. 2002; Dixon 2008; Jefferson et al. 2008). Fraser's dolphins have not been observed in mixed assemblages with bottlenose dolphins, nor would they be expected in the shallow waters (ca. 50 to 100 m deep) in which the PTF operates. In Australian waters, Fraser's dolphins are also regarded as data deficient or insufficiently known (Bannister et al. 1996; Ross 2006; Woinarski et al. 2014).

There are three plausible explanations for the occurrence of the Fraser's dolphin haplotypes among the PTF-associated dolphins. These explanations assume that the information on Genbank for the *Lagenodelphis* haplotypes is correct, i.e. that the published haplotypes originated from Fraser's dolphins. Note, however, that errors have been documented previously on Genbank entries (e.g., Arora et al. 2011). First, both *T. truncatus* and *L. hosei* may have been present in the groups of dolphins that were sampled. The identification of cetaceans in the field can be challenging due to their rapid movements and the at-sea conditions (for example, some biopsy sampling was conducted during the night). Many small cetacean species are distinguished by markings on their flanks, which can be difficult to observe from the bow. A careful re-examination of all photographs taken in the field revealed only the bottlenose dolphin phenotype. The possibility that some individuals were Fraser's dolphins cannot be excluded definitively (having not taken photographs of each individual biopsy sampling event), but no genetic structure was evident in the dataset and the STRUCTURE analysis did not reveal admixed individuals. Thus, there was no indication of having sampled from a mixed population/species assemblage.

Secondly, incomplete lineage sorting may have led to the observed pattern. Under a neutral model of evolution, the stochastic lineage sorting leading to reciprocal monophyly proceeds more slowly in large or rapidly diverging populations. In many groups of species with large population size, such as the Delphinidae (Rice 1998; McGowen 2011), genomes will have mixed support for monophyly unless historical bottlenecks have accelerated coalescence. In biological terms, this means that although the species are reproductively isolated and do not exchange genetic material with one another, similar or even identical

haplotypes may still occur among them, making them difficult to distinguish unambiguously based on mtDNA alone. Use of a greater number of samples from adjacent *Tursiops* and *Lagenodelphis* populations, or use of alternative loci developed for species identification or multiple markers, may assist in resolving such differences in the future (Viricel and Rosel 2012).

A third, albeit remote, explanation for the occurrence of Fraser's dolphin haplotypes among the PTF-associated bottlenose dolphins is that introgression events have taken place, in which Fraser's dolphin mtDNA entered this bottlenose dolphin population through hybridisation. Under such a scenario, female Fraser's dolphins would have mated with male bottlenose dolphins. Successive mating events of female offspring with bottlenose dolphins would lead to a phenotypic appearance of bottlenose dolphins with Fraser's dolphin mtDNA. Hybridisation has been observed frequently in the odontocetes, both in captivity (e.g., Zornetzer and Duffield 2003) and in free-ranging dolphins and porpoises (e.g., Willis et al. 2004; Silva et al. 2005; Brown et al. 2014). A more widespread, geographically representative dataset and further analyses will be required to definitively resolve the reason for the occurrence of Fraser's dolphin haplotypes in the PTF-associated bottlenose dolphins.

3.4.3 Coastal, Indo-Pacific bottlenose dolphins of north-western Australia

All *Tursiops* sampled in shallow (≤ 20 m deep), coastal waters of the north-western Australian coastline were phylogenetically grouped with the Indo-Pacific bottlenose dolphin (*T. aduncus*). The current study also revealed genetic differentiation between *T. aduncus* sampled at the two extreme north-east coastal sites: Beagle Bay (Site 11), which clustered with the rest of the coastal populations to the south-west, and those of Cygnet

Bay (Site 12, < 150 km east, Fig. 3.1). The relatively narrow, deep-water entrance to King Sound, subject to immense tidal movements, may act as a barrier to dispersal. Nevertheless, fine-scale genetic structuring over scales of just tens to hundreds of kilometres should be viewed as the rule rather than the exception in Australian *T. aduncus* (e.g., Wiszniewski et al. 2009; Ansmann et al. 2012b; Kopps et al. 2014), as it should be where either *Tursiops* spp. occupy relatively complex coastal habitats (Fernández et al. 2011; Mirimin et al. 2011; Browning et al. 2014; Fruet et al. 2014; Louis et al. 2014). Additional sample collection to the east of Cygnet Bay may better elucidate the patterns of genetic connectedness among coastal populations of bottlenose dolphins across north-western Australia and whether this is driven by ecological, social or anthropogenic factors.

Tursiops aduncus inhabit near-shore areas of much of the Australian coastline (Ross 2006; Woinarski et al. 2014; this study). Occurring in the shallow, coastal waters of the Western Pacific and Indian Oceans, including north-western Australia, *T. aduncus* thereby occupy a niche otherwise filled by *T. truncatus*, or coastal ecotypes of *T. truncatus*, in various other regions (e.g., the coastlines of New Zealand, the central and Eastern Pacific Ocean, the Western and Eastern Atlantic Oceans, and the Mediterranean Sea – Natoli et al. 2005; Tezanos-Pinto et al. 2009; Fruet et al. 2014). While *T. aduncus* are occasionally caught in coastal trawl fisheries (e.g., Sabah and Sarawak, East Malaysia, Jaaman et al. 2008; Shark Bay, Western Australia, Department of Fisheries 2013), these genetic results clearly show that they are unlikely to be caught in the PTF, since the trawlers operate between ca. 50 and 170 km offshore (beyond the 50 m depth contour) in an open, pelagic environment.

3.4.4 Conclusions and recommendations

Common bottlenose dolphins (*T. truncatus*) interacting with the PTF form part of a relatively large population that is demographically isolated from adjacent coastal populations. The results from this Chapter have clearly demonstrated the lack of genetic exchange or recruitment into the PTF-associated population from adjacent coastal (*T. aduncus*) populations.

The accumulation of a more complete set of samples from pelagic *T. truncatus* would allow: the quantification of the levels of gene flow with adjacent populations; the detection of any changes in population size due to fishery-caused mortalities (c.f. Garza and Williamson 2001); and, the assessment of whether or not closely related individuals are subject to bycatch, which can exacerbate the demographic impacts of bycatch in social species such as delphinids (c.f. Mendez et al. 2010; Wade et al. 2012).

The key findings from this study are:

i. The common bottlenose dolphin (*T. truncatus*) is the predominant species associating with the Pilbara Trawl Fishery;
ii. Haplotype sharing with, or recruitment from, the adjacent, coastal populations of Indo-Pacific bottlenose dolphins (*T. aduncus*) into the PTF does not occur;
iii. There appears to be little or no genetic sub-structuring within the PTF-associated population of *T. truncatus*;
iv. A more complete sample dataset (from offshore populations of *T. truncatus*) should be acquired in order to better-quantify the impact of historical and ongoing bycatch on the PTF-associated population.

v. The coastal *T. aduncus* populations fall into three main clusters. Analysis of samples from further east in the Kimberley might help explain the differentiation found between Beagle and Cygnet Bays in this study.

Appendix 3.1. Sample vouchers from Genbank, species and corresponding references used to provide comparison with the samples collected here.

Genbank Acc. #	**Species**	**Reference**
EF581128	*Tursiops aduncus*	Möller et al. 2008
AF287951	*Tursiops aduncus*	Möller and Beheregaray 2001
AF287952	*Tursiops aduncus*	Möller and Beheregaray 2001
AF287953	*Tursiops aduncus*	Möller and Beheregaray 2001
AF287954	*Tursiops aduncus*	Möller and Beheregaray 2001
AF287955	*Tursiops aduncus*	Möller and Beheregaray 2001
GQ420670	*Tursiops aduncus*	Wiszniewski et al. 2010
HQ115064	*Tursiops aduncus*	Wiszniewski et al. 2010
AF056231	*Tursiops truncatus*	Wang et al. 1999
AF056230	*Tursiops truncatus*	Wang et al. 1999
AF056228	*Tursiops truncatus*	Wang et al. 1999
AF056226	*Tursiops truncatus*	Wang et al. 1999
AF056227	*Tursiops truncatus*	Wang et al. 1999
AF056225	*Tursiops truncatus*	Wang et al. 1999
JN571481	*Tursiops australis*	Charlton-Robb et al. 2011
JN571469	*Tursiops australis*	Charlton-Robb et al. 2011
JN571467	*Tursiops australis*	Charlton-Robb et al. 2011
EU121119	*Lagenodelphis hosei*	Caballero et al. 2008
EU121120	*Lagenodelphis hosei*	Caballero et al. 2008
AF113487	*Lagenorhynchus acutus*	Cipriano 1997

Appendix 3.2. Genetic diversity indices for sampling sites for all 19 microsatellite loci. *N* = number of individuals, *N*a = mean number of alleles/locus, *N*e = mean number of effective alleles/locus, *I* = Shannon's information index, H_O = mean observed heterozygosity over all loci, H_E = mean expected heterozygosity over all loci, uH_E = unbiased mean expected heterozygosity over all loci, *F* = fixation index, SE = standard error of the mean.

Sampling Site	*N*		*N*a	*N*e	*I*	H_O	H_E	uH_E	*F*
1 Useless Inlet	33	Mean	4.579	2.717	1.078	0.582	0.565	0.574	-0.030
		SE	0.537	0.285	0.103	0.044	0.040	0.041	0.018
2 Western Shark Bay	21	Mean	4.684	2.820	1.097	0.596	0.568	0.582	-0.052
		SE	0.508	0.336	0.104	0.043	0.040	0.041	0.028
3 Eastern Shark Bay	53	Mean	5.526	2.851	1.128	0.547	0.565	0.570	0.027
		SE	0.747	0.307	0.116	0.045	0.047	0.048	0.019
4 Dirk Hartog Island	16	Mean	4.526	2.726	1.081	0.566	0.564	0.582	-0.020
		SE	0.504	0.277	0.104	0.041	0.042	0.044	0.036
5 Coral Bay	14	Mean	4.579	2.826	1.138	0.605	0.589	0.611	-0.031
		SE	0.503	0.285	0.098	0.041	0.037	0.038	0.041
6 North West Cape	26	Mean	4.895	2.650	1.079	0.538	0.547	0.557	0.008
		SE	0.512	0.311	0.104	0.042	0.041	0.042	0.035
7 Onslow	6	Mean	4.263	3.086	1.161	0.667	0.608	0.663	-0.112
		SE	0.458	0.385	0.104	0.049	0.037	0.041	0.058
8 Dampier Archipelago	27	Mean	5.211	3.048	1.193	0.610	0.605	0.616	-0.010
		SE	0.544	0.321	0.102	0.040	0.039	0.039	0.023
9 Port Hedland	25	Mean	5.000	2.835	1.148	0.594	0.591	0.603	-0.010
		SE	0.490	0.234	0.099	0.044	0.040	0.041	0.039
10 Cable Beach	17	Mean	4.632	3.240	1.191	0.591	0.613	0.632	0.063
		SE	0.497	0.356	0.114	0.055	0.044	0.045	0.039
11 Beagle Bay	15	Mean	4.737	2.863	1.140	0.632	0.586	0.606	-0.087
		SE	0.438	0.282	0.098	0.041	0.039	0.041	0.023
12 Cygnet Bay	20	Mean	4.421	2.916	1.118	0.563	0.586	0.601	0.028
		SE	0.467	0.293	0.107	0.046	0.044	0.046	0.032
13 NW Cape offshore	3	Mean	3.211	2.702	0.990	0.649	0.556	0.667	-0.174
		SE	0.260	0.242	0.102	0.078	0.053	0.063	0.086
14 PTF West	47	Mean	6.316	3.418	1.305	0.613	0.619	0.626	0.032
		SE	0.649	0.363	0.127	0.059	0.055	0.056	0.039
15 PTF East	21	Mean	5.526	3.633	1.303	0.639	0.627	0.643	-0.028
		SE	0.584	0.434	0.133	0.058	0.057	0.058	0.020

Chapter Four: Estimating the abundance and fidelity of bottlenose dolphins in a demersal trawl fishery

4.0 Abstract

The bycatch of cetaceans in fishing gear presents a global conservation challenge. To inform an assessment of the impact of bycatch on bottlenose dolphins in a north-western Australian trawl fishery: an aerial survey was conducted to estimate dolphin abundance across the fishery in April, 2011; simultaneously, boat-based dolphin photo-identification was carried out to assess short-term fidelity to foraging around trawlers; and opportunistically collected photographic and genetic data were used to infer longer-term fidelity to the fishery. The estimated abundance of dolphins in the four (of five) management areas surveyed based on distance sampling was 1,551 (95% CI = 822-2,929), for a total estimate of ca. 2,300 dolphins in an area of ca. 25,880 km^2 (0.09 dolphins km^{-2}). Short-term mark-recapture estimates based on photo-identification yielded a total of 226 dolphins (SE = 38.5; 95% CI = 162-315) associating with one of three trawlers in the fleet. The mean group size of trawler-associated dolphins was five times higher (mean ± SE = 28.0 ± 3.0; range = 16-46) than that of non-trawler-associated animals (5.0 ± 0.6; 1-30; T_{92} = 12.1; $P < 0.0001$). Individual dolphins were photo-identified up to seven times over two weeks and three distinctive adults were matched with images collected opportunistically in 2008. Similarly, five individuals were genetically matched with samples collected up to 2.5 years earlier. Fifteen years after dolphin bycatch was first reported in this fishery, this study presents the first abundance estimate for any Australian pelagic delphinid, and suggests that the number of dolphins interacting with the fishery is smaller than expected. It also provides photographic and genetic evidence that a proportion of the population repeatedly engage in foraging around trawlers over days, months and years. Considering

these findings, further abundance estimates are needed and the acceptable annual dolphin bycatch limit is in need of revision.

4.0 Introduction

Most cetacean species interact with coastal and offshore fishing operations in at least some of their geographical ranges as both the human population and our demand for seafood grow (Whitehead et al. 2000; DeMaster et al. 2001; Northridge et al. 2003; Read et al. 2003b; Read 2008; FAO 2014). The combination of the direct and indirect impacts from fishing activities has resulted in declines that may be irreversible in many populations, including common dolphins (*Delphinus delphis*) in the Mediterranean Sea, vaquitas (*Phocoena sinus*) in the Gulf of California, finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) of the Yangtze River and Maui's dolphins (*Cephalorhynchus hectori maui*) off New Zealand's North Island (Reeves et al. 2003; Slooten et al. 2006; Jaramillo-Legorreta et al. 2007; Piroddi et al. 2011; Mei et al. 2014). Efforts to mitigate against the incidental capture, or bycatch, of dolphins in the tuna purse seine fishery of the eastern tropical Pacific resulted in massive reductions in mortality rates of spinner (*Stenella longirostris*) and spotted dolphins (*S. attenuata*; Perrin 1969; Hammond 1981; Wade 1995). Despite this apparent success, however, more recent evidence suggests that these populations are not recovering (Gerrodette and Forcada 2005; Wade et al. 2007; Cramer et al. 2008). Furthermore, the incidental and targeted capture of small cetaceans still occurs in numerous regions, despite protective legislation that bans such practices having been in place for decades (e.g., Baur et al. 1999; Read 2008; Mangel et al. 2010; Bilgmann et al. 2014; Song 2014). These examples highlight two of the factors that make effective conservation of cetaceans impacted by fisheries difficult: the life-history traits of cetaceans, being long lived, late maturing and having very low rates of reproduction, make most

populations vulnerable to additional sources of mortality and slow to recover; and effective compliance with policy is difficult to ensure when the economic incentives from fishing discourage a genuine commitment to protected species conservation.

Australia has the third largest Economic Exclusion Zone in the world, in which a number of domestic commercial fisheries operate, including gill netting, purse seining and trawling (Larcombe et al. 2006). These three fishing techniques lead to the greatest proportions of small cetacean bycatch in Australian waters (e.g., Harwood and Hembree 1987; Shaughnessy et al. 2003; Hamer et al. 2008), as they do globally (Read et al. 2006). Australia lacks a specific *Marine Mammal Protection Act* (MMPA), like that in the United States (1972), under which the Potential Biological Removal equation is used to set an upper limit on human-caused mortality to cetacean populations (Barlow et al. 1995; Wade 1998). In Australia, all cetaceans are protected under the *Environment Protection and Biodiversity Conservation (EPBC) Act* (1999). A provision of the *EPBC Act* stipulates that a commercial fishery should receive accreditation to operate and export product only if it does not, or is not likely to, adversely affect the conservation status of a listed migratory species, cetacean, or listed marine species or a population of that species.

Although overall bycatch rates are likely to be decreasing in Australian fisheries, baseline data on the population size and dynamics on the vast majority of cetacean populations, delphinids in particular, are lacking (Ross 2006; Allen et al. 2012; Woinarski et al. 2014). Without information on mortality rates, population sizes or boundaries, it is not possible to assess the level of risk to the viability of cetacean populations subject to fisheries bycatch (Barlow et al. 1995; Taylor et al. 2000; Read 2008). Attempts have been made to estimate cetacean bycatch levels from observer data or implement trials for bycatch reduction

around Australia (e.g., Harwood and Hembree 1987; Stephenson and Chidlow 2003; Stephenson and Wells 2006; Hamer et al. 2008; Lyle and Willcox 2008; AFMA 2011; Chapter 2; Allen et al. 2014), but without abundance estimates or trend data for most cetacean populations, assessing the magnitude of the impact of bycatch on these populations remains beyond reach. Furthermore, understanding these impacts at the population level also requires estimation of total fishing-related mortality rates, which consist of three components: (*i*) animals landed on deck dead; (*ii*) animals landed on deck alive and released, then dying after release; and (*iii*) animals that are not landed on deck, but die after interacting with the fishing gear, e.g., animals that fall out of the fishing gear during fishing or on retrieval of the gear, but are not seen (e.g., Jaiteh et al. 2014).

The common bottlenose dolphin (*Tursiops truncatus*, 'bottlenose dolphin' hereafter) is globally well known and the subject of in-depth research in many locations, but considered data deficient around Australia (Ross 2006; Woinarski et al. 2014). This is likely a result of their occurrence in less accessible, pelagic habitats, while Indo-Pacific bottlenose dolphins (*T. aduncus*) occupy much of Australia's shallow coastal waters (Ross 2006; Chapter 3). No population estimates for bottlenose dolphins exist in Australia and our limited knowledge from north-western Australia is a result of recent research due to their bycatch in the Pilbara Trawl Fishery ('PTF' hereafter, Chapter 2). A bycatch rate of ca. 50 dolphins per annum was first estimated in 2002 (Stephenson and Chidlow 2003). Subsurface behaviour inside actively fishing trawl nets has subsequently been described in some detail (Mackay 2011; Jaiteh et al. 2013), bycatch rates from interacting with the fishery have been estimated (Chapter 2; Allen et al. 2014) and the bottlenose dolphins interacting with the PTF are genetically isolated from the adjacent, coastal populations (Chapter 3).

Independent observer data from 2003 to 2009 also showed a bycatch rate of ca. 50 dolphins per annum, approximately double that reported by skippers, and that the introduction of Bycatch Reduction Devices (BRDs) resulted in fewer dolphins being landed on deck (Chapter 2; Allen et al. 2014). However, skippers' logbook data for 2012 showed that dolphin bycatch has increased above levels reported immediately after BRDs were introduced in 2006 (Department of Fisheries 2013). Video footage collected inside actively fishing trawl nets showed some dolphins being caught and then expelled from the BRDs before winch up (Jaiteh et al. 2013, 2014). Thus, dolphin mortality rates are typically under-estimated in the PTF because of both under-reporting by skippers and the unobserved loss of dead or moribund animals during trawling. In 2012, a further six-month trial of an electronic observer system was conducted to estimate bycatch of dolphins, but this was not verified against independent observer data (Wakefield et al. 2014).

Under-reporting in fisheries statistics, the bycatch of protected species in particular, is a common phenomenon elsewhere around Australia (e.g., Ward et al. 2012) and the world (e.g., Moore et al. 2010). The impact of this incidental mortality remains unknown without estimates of population size or connectivity with adjacent populations (Chapter 2; Chapter 3; Allen et al. 2014). This research was aimed at estimating the total abundance of bottlenose dolphins interacting with the PTF by conducting an aerial survey of the fisheries management areas in April 2011. During the same period, the number and short-term fidelity of dolphins foraging behind one trawler (of three in the fleet) over days to weeks were estimated by employing individual photographic identification capture-recapture methods during two consecutive, one-week fishing trips. Finally, fidelity to foraging around trawlers over periods of months to years was inferred by using photographic and genetic (biopsy sample) data collected opportunistically between

October 2008 and April 2011 in the PTF. This research provides critical baseline information upon which to base an objective assessment of the impact of dolphin bycatch in the PTF.

4.2 Materials and methods

4.2.1 Pilbara Fish Trawl Interim Managed Fishery

The PTF extends from longitude 116ºE to 120ºE and within the approximate boundaries of the 50 m depth contour to landward and the 100 m depth contour to seaward (Fig. 4.1). There are four management areas (1, 2, 4 and 5) open to trawling, covering an area of ca. 23,000 km^2, and one management area (3) closed to trawling. At the time of the aerial survey and photo-identification research described here (April 2011), three vessels were operating in the PTF and the research activities had no influence on fishing operations. Fishing occurs year-round, with temporary breaks in the event of a tropical cyclone in the Austral summer (typically December to March). Fishing trips into the PTF last one to two weeks. From 2010 to 2012, between ca. 7,300 and 10,300 h of trawling were conducted per annum (Department of Fisheries 2013). Further details on annual catches in the PTF can be found in Department of Fisheries (2013), and net characteristics and bycatch rates are reported in Chapter 2, Allen et al. (2014) and Jaiteh et al. (2013, 2014).

4.2.2 Overview of sampling

The data collected and examined in this study include: dolphin counts from an aerial survey in April 2011 (4.2.3 below); photo-identification of dolphins associated with a trawler in April 2011 (4.2.4 below); and opportunistic photo-identification from trawlers in 2008 and 2011, as well as biopsy sampling from around trawlers between 2008 and 2011 (4.2.5 below).

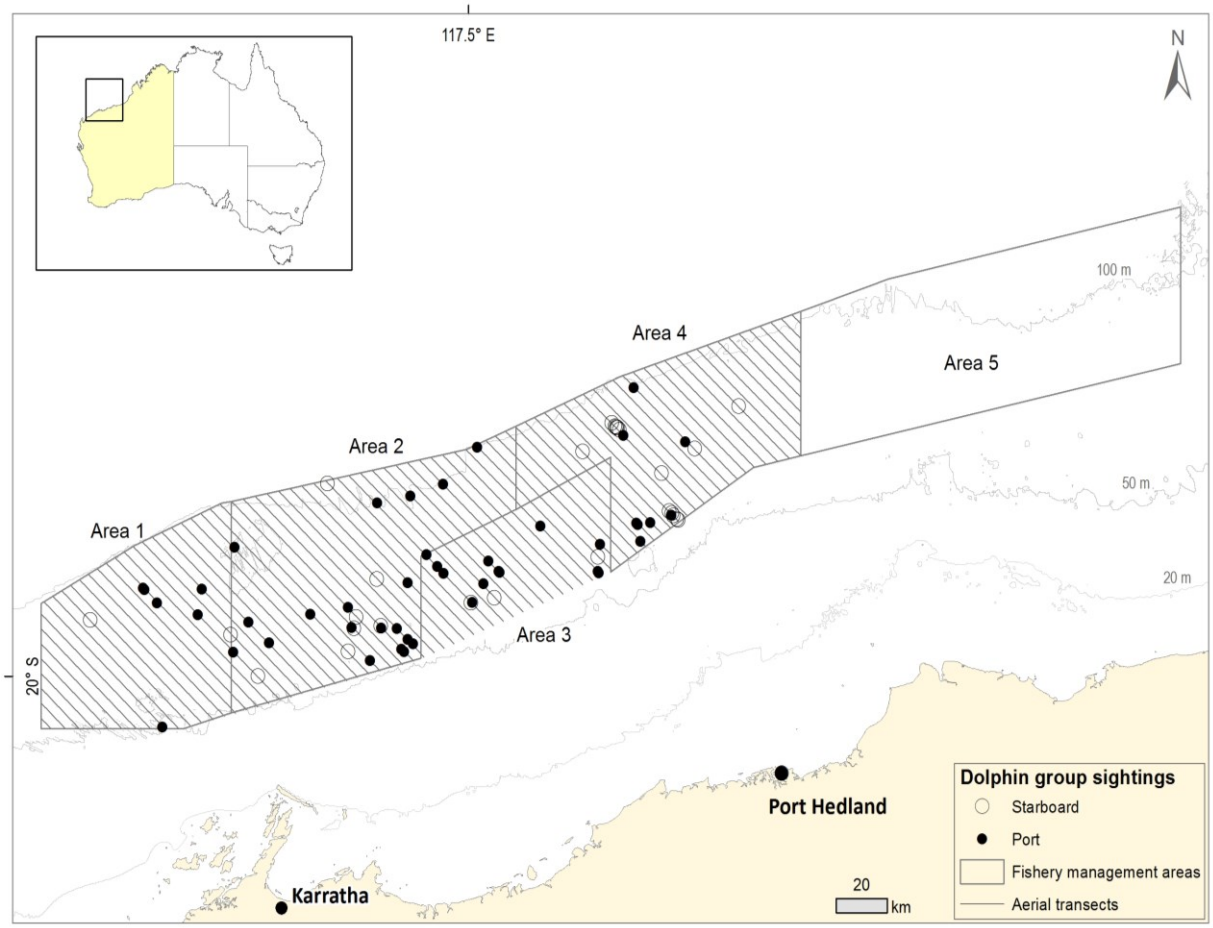

Figure 4.1. Aerial tracks surveyed in 2011 across the PTF. Fishery management areas 1, 2, 3 and 4 were surveyed (trawling is not permitted in area 3; area 5 was not surveyed due to a curtailing of the survey as a result of safety concerns). Circles indicate dolphin sightings (filled = port observer/s, open = starboard observer); 20 m, 50 m and 100 m depth contours are also indicated.

4.2.3 Aerial survey to estimate dolphin abundance in the Pilbara Trawl Fishery

4.2.3a Line transects

Eleven aerial survey flights were carried out between 11th and 23rd April, 2011, in a Cessna C337 (twin engine, overhead wing) aircraft. Four of the five PTF management areas (areas 1, 2, 3 and 4) were surveyed, covering a total area of 18,250 km^2 (Fig. 4.1). A series of 81 transects, oriented NW-SE and spaced 3.7 km (2 nm) apart (combined linear distance = 4,937.4 km), were surveyed by a team of three observers at an altitude of 152.4 m (500 feet) and a cruising speed of 185 km h^{-1} (100 knots), in keeping with accepted standards for aerial surveys of small cetaceans (Dawson et al. 2008). Transects were laid out

according to a systematic design that provided an even coverage probability across the study region.

Survey lines were broadly perpendicular to the nearest coastline and depth contours, and parallel to the expected onshore/offshore density gradient for the species (as recommended by Buckland et al. 2001). The speed of the aircraft was much faster than that of any animal movement, effectively providing a snapshot of abundance of animals at the surface in the area at the time of the survey (Buckland et al. 2004). The average flight time was 3 h 35 min, and the average transect length was 61 km.

4.2.3b Data recording

Personnel for all surveys included two pilots, a data recorder, one starboard observer and two visually and acoustically independent (separated by a dark material curtain and using separate audio channels in the intercom) portside observers (e.g., Marsh and Sinclair 1989; Slooten et al. 2004). Only portside data were used in the mark-recapture distance sampling analyses (see section *4.2.3d*). The observers and data recorder were linked via a separate intercom system and data were logged with a time code to a digital tape recorder. Observers measured vertical angles from the plane to each sighted dolphin group using hand-held clinometers as the animals passed abeam of the aircraft. Based on known heights and vertical angles, perpendicular distances from the plane were calculated using trigonometry (Lerczak and Hobbs 1998).

In addition to perpendicular distance, the following variables were recorded (the first two of which relate to sightings, while the rest to search effort and sighting conditions):

(1) *Group size (S)* - observers provided three estimates (minimum, maximum, best);

(2) *Calves (CA)* - a binary factor coding for the presence (1)/absence (0) of one or more calves within the group;

(3) *Fatigue (F)* - a measure of the time elapsed (in min) since the start of each flight;

(4) *Time of day (T)* - a factor with two levels (morning = AM / afternoon = PM);

(5) *Beaufort sea state (B)* - a factor with two levels ("low" for sea states ≤ 2, "high" if > 2);

(6) *Cloud cover (CC)* - a factor with eight levels (one for each of 8 oktas);

(7) *Glare intensity (G)* - a factor with four levels (0 = no glare, 1 = weak, 2 = moderate, and 3 = high);

(8) *Glare angle (GA)* - the angle of glare within the observers' field of view (e.g., if the glare extends from 270° to 310°, then the GA takes a value of 310-270 = 40°).

All of these variables and some of their interactions were considered as co-variates in the models for estimating detection probability (see below). Surveys were undertaken in passing mode, although a circling protocol was employed upon encountering large (15+ animals) and/or trawler-associated groups, whereby the aircraft deviated from its path and circled the dolphins multiple times to confirm group size, composition and species identification (Slooten et al. 2004; Rayment et al. 2010). Once the group characteristics were confirmed, the flight and data collection along the transect line were resumed.

4.2.3c Duplicate sighting identification

Duplicate sightings are those recorded by two independent observation platforms. Sightings recorded at similar times (within 2.5 seconds, or about 100-150 m in distance) and angles (within five degrees) by the primary (front) and secondary (rear) observers were considered duplicates. For analytical purposes, the angle measurements made by the

primary observers (the more experienced) were considered more reliable than those made by the secondary observer.

4.2.3d Data analysis: Mark-recapture distance sampling (MRDS)

All analyses were carried out using the open-source software package Distance 6.2 Release 1, available from http://www.ruwpa.st-and.ac.uk/distance/ (and see Thomas et al. 2010). As often occurs in aerial surveys of marine animals, the flat windows of the Cessna limited visibility in the vicinity of the flight path. To remedy this, sightings were left-truncated at 100 m (threshold chosen based on a visual inspection of the raw data). Although automatic left-truncation is implemented within Distance 6.2, the software assumes that detection is certain on the trackline and, therefore, extrapolates the detection function back to distance 0. Left-truncation was performed manually (in Microsoft Excel) by discarding sightings located within the first 100 m and subtracting "100" from the measured distances of all remaining data points (as per Borchers et al. 2006). Data were subsequently binned into 75 m intervals and right-truncated at 450 m. All unidentified and trawler-associated clusters of dolphins were excluded from this analysis so as not to unduly inflate the abundance estimates. Mark-recapture distance sampling (MRDS) models were fitted to the dual-observer sightings on the portside to estimate the abundance of available dolphins whilst accounting for any departures from the key assumption (see *4.2.3g* below) that g(0) (detection probability on the trackline) is equal to 1.

A total of 69 plausible candidate models were tested under both assumptions of point (with a half-normal key function) and full independence (Laake et al. 2008; Fewster and Pople 2008). A logistic form was used to derive conditional detection probability functions $p_{1|2}(y, \underline{z})$ (probability that observer 1 detects an animal, given that it is seen by observer 2) and

$p_{2|1}(y, \underline{z})$ (probability that observer 2 detects an animal, given that it is seen by observer 1) (Buckland et al. 2009). The overall probability *p.* that at least one observer detects an animal was then calculated as:

$$p.(y, \underline{z}) = p_1(y, \underline{z}) + p_2(y, \underline{z}) [1 - p_{1|2}(y, \underline{z})]$$

(where z is a vector of explanatory terms and y represents distance) (Buckland et al. 2004).

Models included multiple combinations of covariate main effects and their first-order interactions and were selected based on the Akaike's information criterion (AIC). Since the Distance program for MRDS estimation does not currently enable model averaging, the model with minimum AIC score was retained as the final best model. These models were used to provide the best possible abundance estimate under the constraints of the available data (both in terms of sample sizes and available covariates recorded - Buckland et al. 2004). The MRDS results are presented first, as dual observer data can account for uncertain detection on the trackline to some degree.

4.2.3e Data analysis: Multiple covariate distance sampling (MCDS)

A basic multiple covariate distance sampling (MCDS) analysis was also run, since the MRDS data from the portside were insufficient to obtain fishery management area-specific estimates of abundance. All sightings (from both port and starboard observers) were used, under the same truncation and filtering conditions as in the MRDS analysis detailed above. Only models with a maximum of three covariate terms (other than distance, without interactions) were considered. Model selection was also performed based on the AIC and final abundance values were corrected for incomplete detection on the trackline using the $p(0)$ estimate $N^* = N \times p(0)$, where N^* is the true abundance and N is the abundance obtained if p(0) is assumed to be 1.

There was no a *priori* reason to believe that detectability was influenced by fishing activity for non-trawler-associated dolphins. Given the relatively small available sample sizes, detection functions were modelled from data pooled over the entire region. Encounter rates and density/abundance estimates were, by contrast, calculated in each separate stratum (fisheries management area) and converted into a region-wide estimate based on an area-weighted average of stratum-specific values.

4.2.3f Addressing different cluster sizes in the field and program distance

Dolphins occur in clusters that can vary considerably in size and, therefore, detectability. Clusters, defined here as one or more bottlenose dolphins, were accurately recorded by using experienced observers and employing a circle-back protocol for group sizes of ≥ 15 individuals. This also allowed for species identifications and cluster sizes to be confirmed. Program Distance estimates mean cluster size using the regression method, in which log cluster size is regressed on estimated probability of detection (Buckland et al. 2001). This removes any size bias effect, i.e. larger clusters are easier to detect than small clusters at greater distances, so the simple mean of observed cluster sizes is a positively biased estimate of population mean cluster size. This method also corrects for any bias that might arise if cluster size is underestimated at greater distances, such that the mean observed cluster size would be a negatively biased estimate of population mean cluster size (Thomas et al. 2010).

4.2.3g Assumptions of distance sampling methods

There are three key assumptions in distance sampling: (1) Objects on the line are detected with certainty; (2) Objects do not move; and (3) Measurements are exact (Buckland et al. 2001; Thomas et al. 2010).

These assumptions are addressed in section *4.2.3d*, *4.2.3a* and by using trained, experienced observers and clinometres, respectively (Borchers et al. 2006; Alldredge et al. 2007; Salgado Kent et al. 2012).

4.2.4 Photo-identification to assess short-term fidelity to trawler-associated foraging

4.2.4a Data collection

Bottlenose dolphins have natural markings on their dorsal fins, making individual identification possible (Würsig and Würsig 1977) and allowing the application of photo-identification methods for use in mark-recapture modelling to estimate abundance (e.g., Wilson et al. 1999; Nicholson et al. 2012; Urian et al. 2014). Two consecutive fishing trips on one trawler (of three operating at the time) in the PTF were conducted between the 10th and 25th April 2011, in fishery management areas 4 and 5 (Figs. 4.1 and 4.4). Six of the seven photo-identification days coincided with aerial survey work (between 12th and 23rd April). Twelve, 20-minute photo-identification surveys of individual dolphins were undertaken (six surveys spread over four days during each fishing trip) from a 4.5 m rigid hulled inflatable deployed from the trawler ca. half an hour before winch-up when conditions were favourable (i.e. sufficient light and Beaufort sea state ≤ 3). Mean trawl time in this fishery is ca. 2.7 h (see Chapter 2 and Allen et al. 2014 for further details).

I attempted to randomly photograph all dolphins following the trawler by making three or four passes of the cluster of dolphins during each survey. In addition to the photo-identification data, the following was also recorded at the start and end of each survey: date, time, depth, sea state, cloud cover (in oktas), latitude, longitude, estimated group size (minimum, best and maximum) and group activity (travel/forage/rest/social).

4.2.4b Data processing

Two independent observers processed the photo-identification data from each sampling occasion by first quality grading each image and then cataloguing each distinctively marked individual. The best quality photograph for each individual captured on a sampling occasion was graded for quality in order to minimise misidentification and heterogeneity in capture probabilities (Friday et al. 2000; Gowans and Whitehead 2001). The photographic quality grading protocol used was modified from that in Urian et al. (1999). Accordingly, photographs were given an absolute value score for clarity/focus (2, 4 or 9), degree of contrast (1 or 3), angle of the dorsal fin to the camera (1, 2 or 8), whether the dorsal fin was fully visible (1 or 8), and the proportion of the frame filled by the fin (1 or 5). The individual scores for each category were summed to obtain an overall quality score (QS). Scores of 6 to 7 were considered excellent quality, 8 to 11 good quality and >11 poor quality. Scores for each category, apart from contrast and the proportion of the frame filled by the fin, were weighted so that inadequate quality in one category alone, could push the photograph over the poor quality threshold.

The degree of distinctiveness varies between dorsal fins of individuals and some are not sufficiently marked to be included in capture-recapture analyses, which only pertain to the distinctly marked population (Wilson et al. 1999; Read et al. 2003a). Each individual in the catalogue was therefore given a distinctiveness score, based on the amount of information contained on the leading and trailing edges of the dorsal fin. Only marks visible from both sides of the dorsal fin were used for identification, so that identifications made from photographs from either side of the dorsal fin could be included in the analyses. Urian et al.'s (1999) distinctiveness protocol was used to grade dorsal fins. Very distinct fins with features evident from distant or poor quality photographs were given a score *D1*;

fins with an average amount of information (one larger or several smaller nicks) were given a score of *D2*; and fins with no, or very little, information a score of *D3*. Every individual was compared to all others in the catalogue before being assigned with a unique identification code and included in the catalogue.

4.2.4c Mark-recapture modelling description

Various capture-recapture models to estimate the abundance of trawler-associated dolphins were run using program MARK (White and Burnham 1999), starting with:

(1) The simplest closed models over all 12 sampling periods, given the surveys were conducted over only two weeks. Models $M_{(t)}$ and $M_{(th)}$ were fitted to allow for any time (t) and individual variation (h) in capture probabilities.

(2) While the study was short, a lack of population closure was to be expected due to the spatial nature of the sampling. A standard open model was therefore fitted using the Popan procedure in MARK (White and Burnham 1999; Williams et al. 2002).

(3) One drawback of the open models is that they do not allow for temporary emigration, which may have occurred here. Hence, Robust Design models were also fitted, which allow for temporary emigration. Using the full data set, the 12 sampling events were grouped into five primary periods (1 = 1, 2, 3; 2 = 4, 5; 3 = 6, 7, 8; 4 = 9, 10; and 5 = 11, 12) by spatial proximity. Furthermore, a reduced data set of 10 survey events was grouped into four primary periods (1 = 1, 2, 3; 2 = 4, 5; 3 = 7, 8; and 4 = 9, 10) by temporal proximity (i.e., days within which multiple sampling events occurred).

4.2.4d Proportion of distinctly marked trawler-associated dolphins

The proportion of distinctly marked individuals ($\hat{\theta}\,\hat{P}_m$) in the population was estimated as the proportion of photographs showing a distinctly marked (*D1* and *D2*) individual from a random sample of 300 good quality (QS < 12) photographs. With this estimation, I assumed that photographs were taken randomly during each sampling occasion. Some bias may have been introduced, however, by a tendency to focus on more distinctly marked individuals. Calves were excluded from this estimation.

4.2.4e Total abundance of trawler-associated dolphins

The population size estimates from the capture-recapture models relate to the distinctly marked population. To estimate the total population size at a particular time, these estimates were adjusted to take into account the proportion of individuals in the population that are unmarked:

$$\hat{N}_{total} = \hat{N}_m / \hat{\theta}.$$

Here, $\hat{N}_{total}$ is the estimated total population size, $\hat{N}_m$ the estimated distinctly marked population size and $\hat{\theta}$ the estimated proportion of distinctly marked individuals in the population. The approximate variance for the estimated total population size was derived using the following formula for the standard error of a ratio:

$$SE(\hat{N}_{total}) = \sqrt{\hat{N}_{total}^{\,2}\left(\frac{SE(\hat{N}_m)^2}{\hat{N}_m^{\,2}} + \frac{1-\hat{\theta}}{n\hat{\theta}}\right)}$$

using the delta method (Williams et al. 2002). Log-normal 95% confidence intervals were calculated with a lower limit of $\hat{N}^L_{total} = \hat{N}_{total}/C$ and upper limit of $\hat{N}^U_{total} = \hat{N}_{total}\, x\, C$, where:

$$C = \exp\left(1.96\sqrt{\ln\left(1+\left(\frac{SE(\hat{N}_{total})}{\hat{N}_{total}}\right)^2\right)}\right)$$ (Burnham et al. 1987).

4.2.4f Addressing the assumptions of the Robust Design method

The assumptions of this application of the Robust Design method were:

(1) All individuals had equal probability of being captured within a secondary sampling occasion,

(2) Capture and recapture probabilities were equal (no trap response),

(3) Marks were unique, permanent and identified correctly,

(4) The sampling interval for a secondary sample was instantaneous,

(5) The population was closed within primary periods,

(6) All individuals have equal probability of survival, and

(7) Each individual's probability of capture was independent of all others (Pollock et al. 1990; Williams et al. 2002).

Regardless of the sampling methods used, the assumption of all individuals having equal probability of capture is not often met for cetacean populations (Hammond 1986). In this study, however, the "population" being "captured" was an aggregation of dolphins foraging behind a trawler. All individuals attracted to the trawler were likely to have had an equal probability of being photographed ("captured"). The assumption of the first capture and then recapture probabilities being equal was considered valid as photo-identification does not require physical capture or handling of animals (Parra et al. 2006). Capture probabilities can be heterogeneous because of an individual's age, sex or social status, and some individuals may be more distinctly marked than others. Such sources of heterogeneity were minimized by; conducting three to four repeated passes of the aggregations of dolphins behind the trawler in each 20-min sampling occasion; by including only captures from excellent- and good-quality photographs; and by including only sufficiently marked individuals in the analyses (Nicholson et al. 2012). The secondary

sampling intervals were considered instantaneous and population closure within primary periods was assumed, given their brief duration and spatial and temporal proximity relative to bottlenose dolphin life history and ranging characteristics. Finally, pelagic bottlenose dolphin populations are not known to be socially structured to the extent of coastal populations (Connor et al. 2000) and our protocol was such that capturing (i.e., photographing) a particular individual would be unlikely to effect the chance of capturing its close associates.

4.2.5 Opportunistic photograph and repeat biopsy sample matching between years to infer long-term fidelity to the PTF

Individual dolphins photo-identified in April 2011 were compared with opportunistically collected photographs from two previous trips, ranging in duration from seven to ten days, aboard two of the three fishing trawlers in October and November 2008. Furthermore, opportunistically collected biopsy samples collected on several trips between October 2008 and April 2011 were used to support the photographic data in assessing fidelity to the region and foraging around trawlers over period of months to years.

Small tissue samples were collected with the PAXARMS remote biopsy system (Krützen et al. 2002) or using a biopsy pole (Bilgmann et al. 2007). All samples were stored in salt saturated 20% Dimethyl Sulfoxide and then sent to the Evolutionary Ecology Group at the University of Zurich (for detailed genetic methods, see Chapter 3). The software microsatellite toolkit (Park 2001) was used to determine identical genotypes among all sampled individuals. Sampling locations of those individuals that were re-sampled at least one day after their initial sampling were plotted within the managed fishery areas with the time and distance between sampling events displayed.

4.3 Results

4.3.1a Aerial survey: Mark-recapture distance sampling

A total of 82 non-trawler-associated bottlenose dolphin clusters were counted (with high confidence) during the aerial survey, ranging in size from 1 to 30 individuals (mean ± SE = 5.0 ± 0.6). Over 90% of the groups/clusters (74) contained 1-10 individuals, while three contained 11-14, and five clusters contained between 15 and 30 dolphins. After truncation and data filtering (see methods), a total of 61 separate dolphin groups were recorded over all surveys. Of these, 36 sightings were made by the dual observer team and were retained for mark-recapture distance sampling (MRDS) analysis (28 detections by observer 1; 26 detections by observer 2; and 18 duplicate detections - Table 4.1).

Table 4.1. Summary statistics from the mark-recapture distance sampling analysis of dolphin data: $n_{1,2}$ is the number of detections made by observers 1 and 2, respectively; n_3 is the number of duplicate sightings; $n_.$ is the total number seen, calculated as $n_1 + n_2 – n_3$; and the p_s are the conditional detection probabilities. Results are in 75 m distance intervals away from the transect.

Distance (m)	$\mathbf{n_1}$	$\mathbf{n_2}$	$\mathbf{n_3}$	$\mathbf{n_.}$	$\mathbf{p_{1\|2}}$	$\mathbf{p_{2\|1}}$
0-75	7	10	7	10	0.70	1.00
75-150	12	7	6	13	0.85	0.50
150-225	5	4	4	5	1.00	0.80
225-300	1	2	0	3	0.00	0.00
300-375	2	2	1	3	0.50	0.50
375-450	1	1	0	2	0.00	0.00
Total	28	26	18	36		

All Full Independence (FI) models exhibited lower AIC scores and were, thus, preferred over Point Independence (PI) models. While PI models have generally been favoured as more robust than their FI equivalent in the literature, FI models can prove equally as appropriate (or more so) in a number of situations (e.g., Buckland et al. 2004, 2009; Collier et al. 2013). Smaller sample sizes favour the simpler models with the stronger assumptions. In these conditions, fitting a PI model can lower bias, but it reduces precision and requires the estimation of more parameters and is, thus, more costly.

A total of 38 MRDS models, ranging in complexity from single main factors to multiple factors with interaction terms, were fitted to the aerial survey data (Appendix 4.1). The best FI MRDS model (with an AIC value of 110.2) contained a glare angle (GA) term, a time of day term (T) and a fatigue term (F), yielding an estimated abundance of 1,551 individuals with an associated 95% confidence interval of 822-2,929 (Table 4.2; Appendix 4.1). Note that, although this was our final choice, a number of other candidate models (e.g., containing cluster size (S) or glare intensity (G) terms, and/or interactions) had AIC values within three of this best model and would, thus, represent viable alternative models (Table 4.2). The best estimates of abundance across the fishery ranged from 1,430 to 1,989 for the eight models within three AIC units of the best model.

The average trackline detection probability *p(0)* for each observer was 0.834 and 0.962 for both observers combined (Fig. 4.2). The estimated *p(0)* is only marginally lower than 1 and a standard conventional distance sampling analysis (with a constrained half-normal key function) yielded a comparable abundance estimate of 1,596 animals (cf. below), albeit with a small gain in precision (95% CI = 932-2,736).

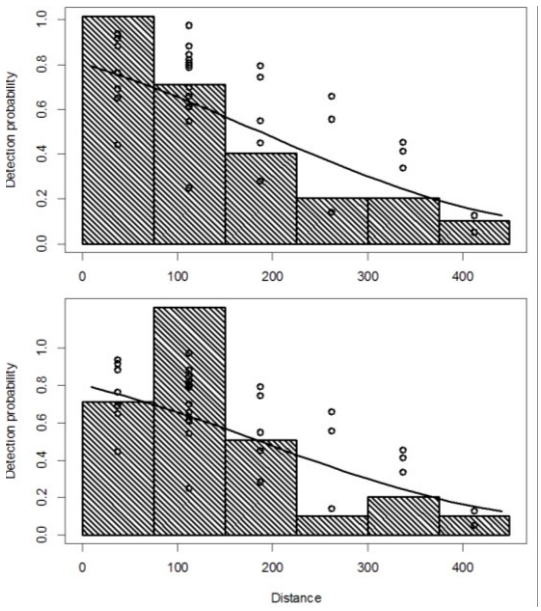

Figure 4.2. Fitted detection probability models for observer 2 (top) and observer 1 (bottom).

Table 4.2. Point Independence (PI) and Full Independence (FI) model details and selection results for the mark-recapture distance sampling analysis of bottlenose dolphin dual observer data. The model for the conventional detection function $g_{.}(y, \underline{z})$ is only relevant in the PI scenario. The best PI and FI models (selected based on AIC scores) are shown in bold; along with eight other models that had AIC values within three of the best model. Details for all 38 models are shown in Appendix 4.1. Covariate terms are as follows: Dist = distance, F = fatigue, G = glare intensity, GA = glare angle, S = group size, T = time of day. Colons ":" code for variable interactions. Derived parameters include animal density (D), abundance (N) and 95% CI (N_{low}; N_{high}).

Model	**Point Independence**							**Full Independence**					
	$g_{.}(y, \underline{z})$	**N**	**N_{low}**	**N_{high}**	**D**	**AIC**	**ΔAIC**	**ΔAIC**	**N**	**N_{low}**	**N_{high}**	**D**	**AIC**
Dist+T+F	**S**	**1,653**	**1,006**	**2,716**	**0.09055**	**193.2**	**83.0**	1.2	1,484	814	2,705	0.08129	111.4
Dist+T+G	S	1,680	1,017	2,776	0.09205	195.0	84.8	2.9	1,578	818	3,046	0.08647	113.1
Dist+T+GA	S	1,651	1,003	2,716	0.09043	193.5	83.3	2.7	1,430	790	2,587	0.07835	112.9
Dist+T+F+S	S	1,650	1,004	2,711	0.09040	195.2	85.0	2.7	1,473	810	2,679	0.08072	112.9
Dist+T+F+GA	S	1,656	1,006	2,728	0.09075	193.7	83.5	**0.0**	**1,551**	**822**	**2,929**	**0.08499**	**110.2**
Dist+T+F+G	S	1,679	1,016	2,776	0.09201	196.3	86.1	2.8	1,633	833	3,203	0.08948	113.0
Dist+T+F+GA+F:T	S	1,657	1,005	2,733	0.09079	195.7	85.5	2.1	1,551	821	2,930	0.08497	112.3
Dist+T+F+S+S:F	S	1,762	972	3,193	0.09654	193.6	83.4	3.0	1,855	646	5,325	0.10163	113.2
Dist+T+F+GA+S+S:F	S	1,768	964	3,243	0.09687	194.3	84.1	2.3	1,989	640	6,182	0.10899	112.5

The area surveyed (management areas 1-4) represents 71% of the total PTF, so the most robust estimate from the MRDS analysis (N; N_{low}-N_{high} = 1,551; 822-2,929) was scaled by area to estimate the number of dolphins across the entire PTF (inclusive of management area 5), yielding 2,185 (1,158-4,125) dolphins. Note that this assumes that the density of dolphins in area 5 is the same as it was estimated to be in other managed areas of the PTF. Furthermore, three groups of trawler-associated dolphins (totalling 89 individuals) were sighted during the aerial survey and excluded from the analyses, so as not to inflate the abundance estimate. These numbers were added to the estimated abundance (as well as the scaled N_{low} and N_{high}) from the aerial survey of non-trawler associated dolphins, which gives a total abundance estimate for the PTF (including management area 3, management area 5 and trawler-associated dolphins) of 2,274 (1,247-4,214) dolphins.

4.3.1b Aerial survey: Multiple covariate distance sampling

Estimates of the number dolphins in the PTF were also calculated using all sightings with a maximum of three covariates. Both half-normal (HN) and hazard rate (HZ) key functions were tested for the detection function, however, the former showed a lower AIC score and was, therefore, preferred (Table 4.3). Example detection functions are given in Fig. 4.3.

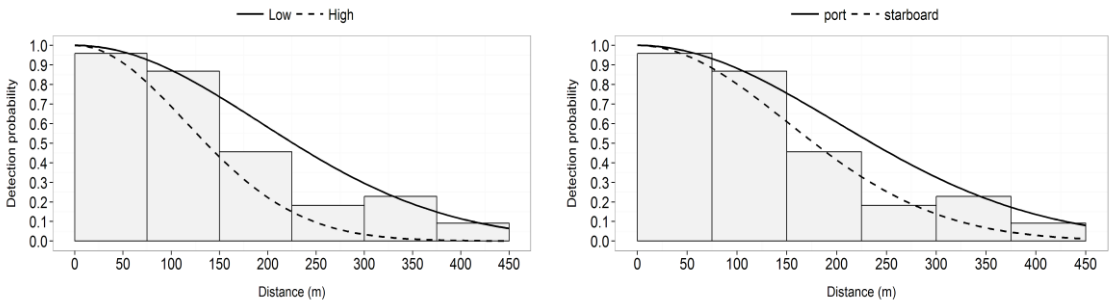

Figure 4.3. Fitted detection functions for bottlenose dolphins surveyed in the Pilbara Trawl Fishery, overlaid on histograms of total sightings. Lines (dashed & solid) indicate different levels of the factor variables Beaufort sea state (left) and Side of the aircraft (right), respectively.

Table 4.3. Model details and selection results from the multiple covariate distance sampling analysis of bottlenose dolphin sighting data in the Pilbara Trawl Fishery. The best models (according to AIC) are shown in bold. Explanatory variables are given in the first column, with Dist=distance, B=Beaufort sea state, CA=calf presence, CC=cloud cover, F=fatigue, T=time of day, S=Group size, SI=side of the aircraft, and GA=glare angle (on the portside). Key functions include a constrained half-normal (HN) and hazard rate (HZ). Derived parameters include the effective strip half-width (ESW, in m), animal density (D) and animal abundance (N). N_{low} and N_{high} represent the lower and upper bounds of the associated 95% confidence interval. CV is the corresponding coefficient of variation.

	Model formula	**Key**	**ESW**	**D**	**N**	**N_{low}**	**N_{high}**	**CV (%)**	**AIC**	**ΔAIC**
1	Dist	HN	221.5	0.108	1,977	931	4,197	39.5	190.68	1.25
2	Dist	HZ	211.9	0.115	2,098	954	4,612	41.6	191.00	1.57
3	**B**	**HN**	**214.0**	**0.116**	**2,126**	**1,003**	**4,510**	**39.5**	**189.78**	**0.34**
4	CA	HN	215.6	0.109	1,996	935	4,264	39.9	190.71	1.28
5	CC	HN	203.0	0.115	2,096	979	4,487	40.0	191.88	2.45
6	F	HN	221.4	0.108	1,973	933	4,172	39.3	192.65	3.22
7	T	HN	221.4	0.109	1,981	937	4,188	39.3	192.67	3.24
8	S	HN	218.1	0.112	2,039	963	4,315	39.4	191.11	1.68
9	SI+T	HN	217.5	0.111	2,027	957	4,293	39.4	192.90	3.46
10	**B+CA**	**HN**	**207.8**	**0.118**	**2,161**	**1,009**	**4,627**	**40.0**	**189.43**	**0.00**
11	B+T	HN	208.1	0.119	2,167	1,015	4,628	39.9	191.74	2.30
12	B+F	HN	213.7	0.116	2,123	1,000	4,505	39.5	191.63	2.20
13	B+SI	HN	212.3	0.118	2,160	1,018	4,585	39.5	191.01	1.58
14	B+GA	HN	212.0	0.116	2,126	1,001	4,514	39.6	190.89	1.46
15	B+S+CC	HN	190.2	0.123	2,253	1,046	4,852	40.4	191.66	2.23
16	B+CA+F	HN	207.8	0.118	2,159	1,008	4,625	40.1	191.43	1.99
17	B+F+T	HN	213.5	0.118	2,156	1,016	4,576	39.5	191.54	2.11

The MCDS model estimates were similar in magnitude to those from the MRDS, abundance estimates ranging from 1,973 to 2,253 for the best models. The best MCDS model (AIC = 189.4) was that which incorporated terms for Beaufort sea state (B) and calf presence (CA). This model was, however, virtually identical to one with Beaufort sea state only (AIC = 189.8). Given the low number of calves encountered during the surveys, the latter was chosen as the preferred model. The total abundance of dolphins in the area

surveyed was estimated at 2,126 dolphins (95% CI = 1,003 - 4,510; CV = 0.395), slightly larger than the estimate from the best MRDS model. Fisheries management area 2 had the highest density of dolphins, whilst area 1 was the least populated of all areas at the time of the aerial survey and area 3 had intermediate abundance estimates (Table 4.4).

Table 4.4: Fisheries management area specific estimates of dolphin numbers.

Management area	N	95% CI	CV
1	140	32-613	0.841
2	802	377-1703	0.398
3	453	172-1187	0.514
4	732	262-2043	0.553

Note that, ideally, transect lines should have been designed independently in each area for robust stratification (strata boundaries were known in advance). Here, the PTF-wide tracklines were split and re-labelled by fisheries management area post-survey and all sightings were re-allocated to the 'new' stratum-level transects via a spatial (nearest neighbour) join algorithm. In doing so, it is possible that the estimates of encounter rate variance in each stratum were artificially inflated. In line transect studies, encounter rate estimators usually dominate the overall variance of object density, and are also the more difficult components to estimate. Given the high levels of uncertainty underlying stratified abundance estimates (particularly for Area 1), their interpretation should be approached with caution. These should be seen more as relative measures of the number of animals in each management area at the time rather than pure, absolute values.

4.3.2 Photo-identification to assess fidelity to trawler-associated foraging

About 1,400 photographs of dolphins were taken during the 12, 20 min surveys conducted on two fishing trips on one trawl vessel over two weeks. A catalogue of 150 individually

recognisable trawler-associated dolphins was constructed; with a total of 327 individual 'captures'. Dolphins were always present following the trawler and their group sizes ranged from 16 to 46 individuals, with a mean group size (± 1 S.E.) of 28.0 ± 3.0. These results are similar to the mean group size of the three aerial survey sightings of trawler-associated dolphin groups (29.7 ± 13.9) and were significantly greater than the mean group size of non-trawler-associated dolphin group (5.0 ± 0.6; n = 82; $T_{92} = 12.1$; $P < 0.0001$).

The individual sighting frequencies ranged from one to seven in the 12 capture periods, with 100 individuals photographed once or twice and 50 identified three to seven times (Fig. 4.5). When only high quality photographs and distinct fins were included, 76 captures and 14 individuals were removed from the dataset. When the remaining 251 captures of 136 distinctly marked individuals were included in the analyses, abundance estimates for all 12 capture periods ranged from 170 ± 8.7 to 210 ± 35.5 marked individuals for the three population models (Table 4.5). Using the full data set, the 12 sampling events were grouped into five primary periods by spatial proximity (Fig. 4.4; Table 4.6a). Further, a reduced data set of 10 events was grouped into four primary periods by temporal proximity (days within which multiple sampling events occurred; Table 4.6b).

The proportion of distinct individuals in the population, or $\hat{\theta}$, was estimated to be 0.93. Using the number of marked animals estimated from the popan model (Table 4.3), the total abundance of trawler-associated dolphins over the sampling period, or $\widehat{N}_{total}$, based on the super population estimate, was 226 (SE = 38.5, 95% CI = 162-315) dolphins.

Table 4.5. Comparison of the estimated population size ($\widehat{N}$), standard error (SE) of the estimate and 95% confidence limits for closed and open models using the photo-identification mark-recapture data to estimate the size of the community of trawler-associated dolphins over the two fishing trips (12 samples) in the Pilbara Trawl Fishery in April 2011. Three population models were used: $M_{(t)}$ = allowing for variation in capture probability with time; $M_{(th)}$ = allowing for both time and individual heterogeneity in capture probability; and Popan = an open population model, assuming closure within sampling days. Open population model runs do not allow for temporary emigration.

Model	$\widehat{N}$	SE($\widehat{N}$)	Graded 95% lower	95% upper
$M_{(t)}$	170	8.7	157	191
$M_{(th)}$	195	17.7	170	241
Popan	210	35.5	166	317

Table 4.6. Comparison of "population" size estimates using Robust Design models with a) the full data set spatially clustered into five primary periods and b) a reduced data set temporally clustered into four primary periods to estimate the abundance of dolphins associating with the trawler over the two-week sampling period. Closure is assumed in each primary period.

Parameter	$\widehat{N}$	SE($\widehat{N}$)	95% lower	95% upper
a) Spatially clustered samples				
Period 1	23.0	0.0	23.0	23.0
Period 2	45.1	9.7	34.1	76.1
Period 3	93.7	17.6	70.9	144.1
Period 4	52.1	14.7	35.3	99.2
Period 5	74.4	9.4	62.7	102.1
b) Temporally clustered samples				
Period 1	23.0	0.0	23.0	23.0
Period 2	45.8	11.8	33.5	85.9
Period 3	88.2	23.1	60.9	159.7
Period 4	38.3	8.2	29.8	66.4

4.3.3 Opportunistic photograph and repeat (biopsy) samples to infer medium- to long-term fidelity to the Pilbara Trawl Fishery

The photo-identification surveys conducted over two fishing trips in April 2011 were concentrated in the centre and east of the fishery (management areas four and five, Fig. 4.4, top left frame). Eight dolphins were photographed between five and seven times during the April 2011 surveys (Fig. 4.4). Three dolphins that were photo-identified on three surveys in April 2011 (Fig. 4.4, bottom three frames) were matched with images collected opportunistically from the stern of trawlers in October and November 2008.

Five individual dolphins were biopsy sampled up to 2.5 years later following their initial sampling on different trips to the PTF. Although repeated sampling of individuals was unintentional, this provided us with the opportunity to infer site fidelity over months and years for at least some individuals. The distances between repeat biopsy-sampling events ranged from 15 km to 140 km and were not related to the time between sampling (Fig. 4.5). The individual with the longest period between sampling events (2.5 years) was re-sampled only 15 km from the initial sampling location (Fig. 4.5). Some individuals were sampled first from one trawler and, later, from another trawler in the fleet of three operating within the PTF.

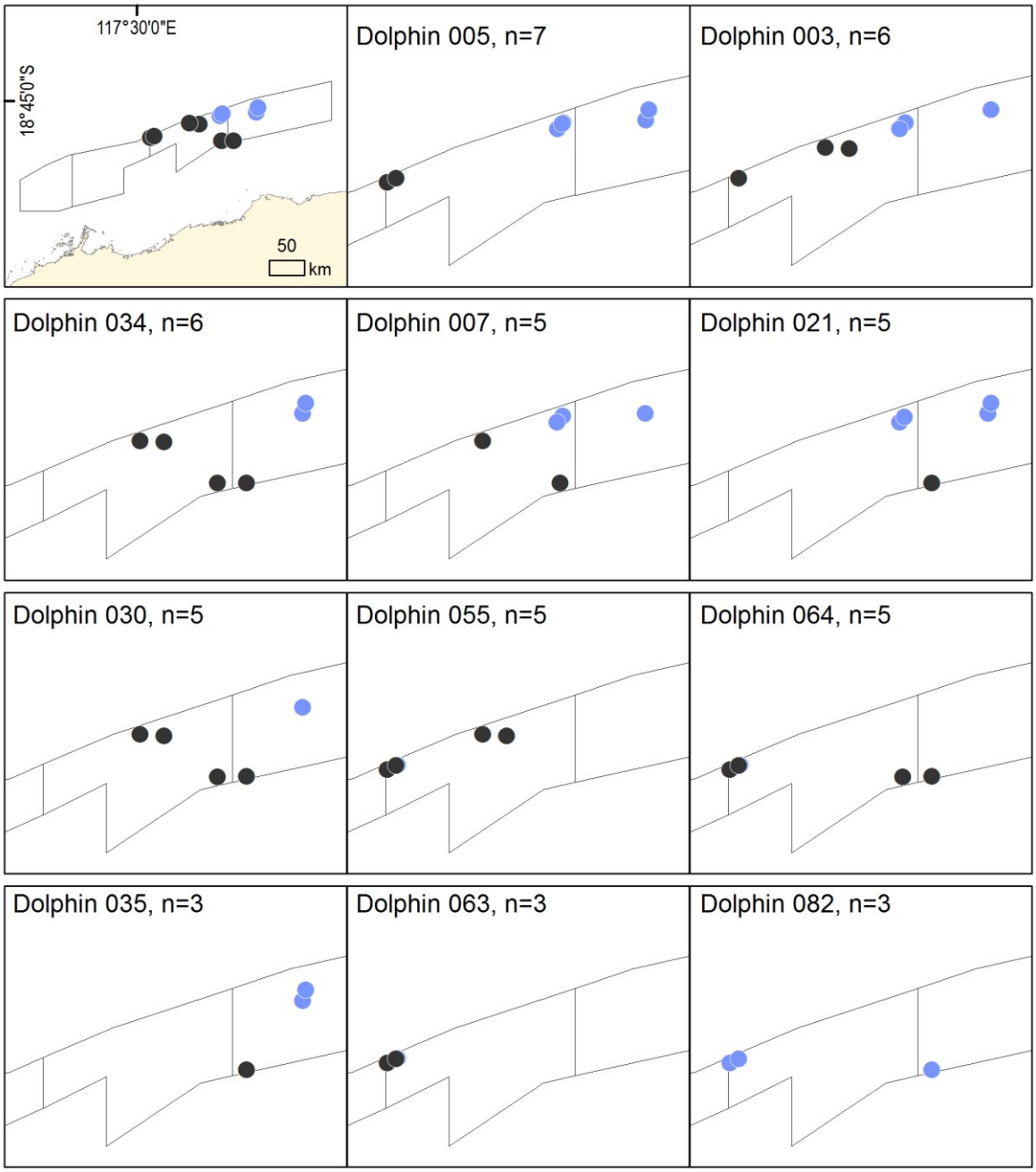

Figure 4.4. The location of the 12 photo-identification surveys conducted during trawling operations in April 2011 (top left frame) and the photographic captures/recaptures of the eight individuals sighted five to seven times (blue circles = trip 1; black circles = trip 2). Also shown in the bottom panels are the locations of the three individuals (dolphin identification numbers 035, 063, and 082) sighted three times in April 2011 that were matched with opportunistically collected images taken in October and November 2008. Note the change in scales between the top left panel and all other panels. Top left panel shows the location of the 12 surveys and the five managed areas of the Pilbara Trawl Fishery; all other panels show only those areas where dolphins were re-photographed (recaptured), primarily managed areas three to five.

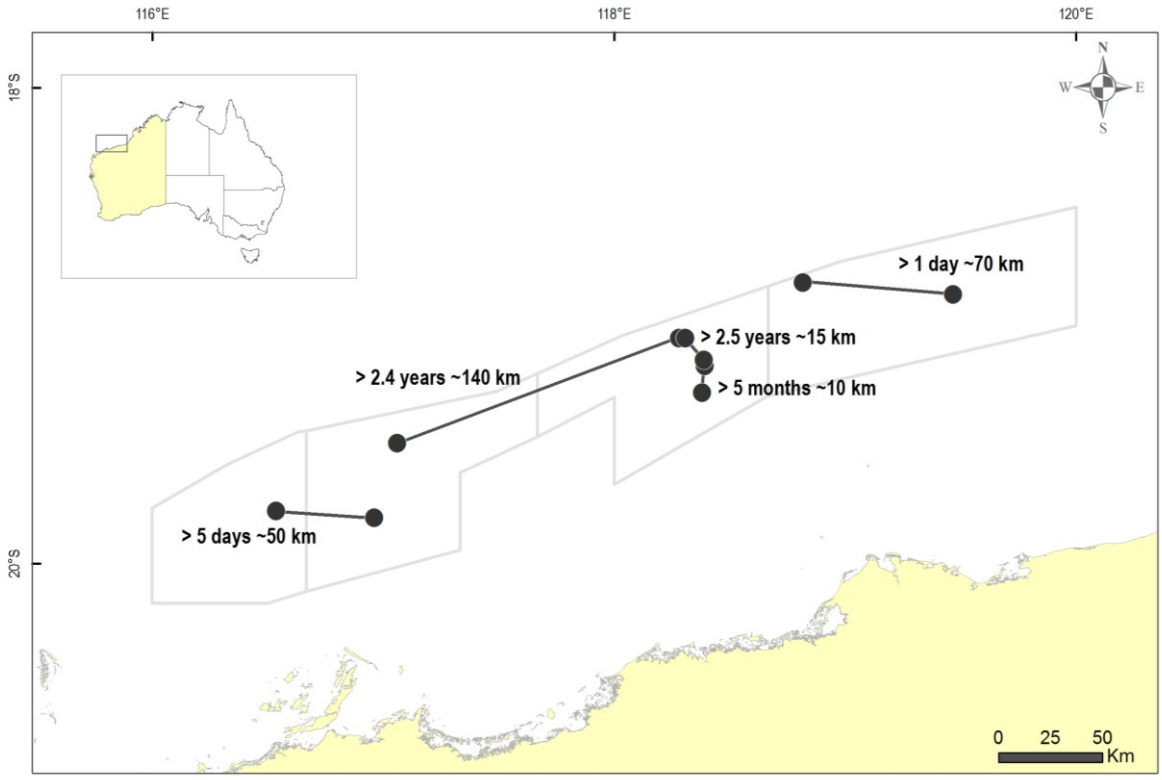

Figure. 4.5: Locations, times and distances between repeat biopsy sampling events of the same five individuals (revealed by genetic identity analyses based on microsatellite data, Chapter 3) taken at least one day following initial sampling (approximate time and distance between sampling events indicated). Lines join circles representing the same individuals (n = 5).

4.4 Discussion

4.4.1 Abundance of bottlenose dolphins in the Pilbara Trawl Fishery

Some 15 years after dolphin bycatch was first reported in the Pilbara Trawl Fishery (Department of Fisheries 2000), this study presents the first abundance estimate for pelagic bottlenose dolphins (*Tursiops truncatus*) interacting with an Australian fishery. Indeed, this is the first abundance estimate for any pelagic delphinid in Australian waters. The lack of other such estimates precludes regional comparisons of population sizes in Australasia. Although the estimate from the mark-recapture distance sampling (MRDS) can capture some degree of perception bias, there are no correction factors for availability bias based on independent data of surfacing intervals for dolphins in Australian waters. Since availability bias was unable to be corrected for explicitly (due to the proportion of dolphins

deeper than observers can detect below the surface), the result is likely to be an under-estimate of the number of dolphins in the area at the time. Slightly larger estimates to those from the MRDS were obtained using the multiple covariate distance sampling. Estimates of ca. 2,000 to 3,000 dolphins in 25,880 km^2, or ca. 0.1 dolphins/km^2, interacting with the PTF are, nevertheless, lower than expected based on the findings from other regions.

Aerial surveys of a similar-sized area (26,700 km^2) in the Gulf of Mexico, USA, for example, resulted in an estimate of 5,141 bottlenose dolphins (0.19 dolphins/km^2; Waring et al. 1999), or about double the abundance of dolphins interacting with the PTF. There were similar numbers of bottlenose dolphins (2,225) in the Mississippi Sound, USA, to the numbers interacting with the PTF, but they occupied an area of < 10% (2,104 km^2; Miller et al. 2013) of that of the PTF. Even taking seasonal fluctuations in habitat use into account, the dolphin density in the offshore areas of the Mississippi Sound (Miller et al. 2013) were two to three times the density of those in the PTF.

There are also a number of abundance and density estimates for bottlenose dolphin populations inhabiting various parts of the Mediterranean Sea that are similar in magnitude to, or smaller than the densities estimated for the PTF (e.g., Forcada et al. 2004; Cañadas and Hammond 2006). This is likely to be explained by a combination of centuries of overfishing, targeted 'fishing' for dolphins of varying magnitudes in some areas, habitat degradation through coastal development and, more recently, increasing commercial and recreational vessel traffic (e.g., Bearzi et al. 2004, 2006; Lauriano et al. 2014). The PTF is sparsely populated and remote by comparison to the Mediterranean and only in the last few decades, subject to the pressures of industrialised anthropogenic activity (Bejder et al. 2012).

Whether or not the population size of bottlenose dolphins in the PTF fluctuates seasonally is unknown, but no temporal variations were detected in the rates of dolphin bycatch among seasons (Chapter 2; Allen et al. 2014). Other than the occurrence of occasional cyclones between December and April, this tropical, pelagic environment is likely to be more constant throughout the year than coastal waters, where seasonal changes in temperature are greater. This is particularly so in temperate latitudes, where significant seasonal changes in the abundance of Indo-Pacific bottlenose dolphins (*T. aduncus*) have been detected (e.g., Smith et al. 2014).

There is a perception by the fishing industry and managers that the dolphin population size is very large, which may have arisen from observations of the numbers of dolphins behind trawlers toward the end of each trawl (along with the assumption that these were 'new' dolphins each trawl) during the various bycatch surveys reported for the PTF (e.g., Stephenson and Chidlow 2003; Wakefield et al. 2014). Indeed, independent observers estimated group sizes at the time of winch-up of 25-50 dolphins (Jaiteh et al. 2013) and, in the current study; group sizes of 16-46 individuals were documented around trawlers. This study also showed that the mean group size (28) of trawler-associated dolphins was five or more times greater than that of dolphin groups observed from the air and not in the vicinity of trawlers (5). Furthermore, the aggregations of dolphins observed behind trawlers repeatedly include a proportion of the same individuals (see *4.4.2* below). Also, Indo-Pacific bottlenose dolphins (*T. aduncus*), which may appear to be the same species as those associating with the PTF (*T. truncatus*), are often seen in north-western Australian coastal waters (Allen et al. 2012). The results from the genetic analyses in Chapter 3, however, illustrate that the dolphins interacting with the PTF are a different species and genetically isolated from the coastal Indo-Pacific bottlenose dolphins populations, and this

study shows the number interacting with the PTF to be relatively small. Determinations that "Given the area of distribution and expected population size of these protected species, the impact of the trawl on the stocks of these protected species is probably minimal"; that < 75 dolphin mortalities year^{-1} is an "acceptable" limit; and that mortalities from bycatch pose "negligible risk" to the dolphin population (Department of Fisheries 2004, 2013; Wakefield et al. 2014), appear to be overly optimistic.

4.4.2 Fidelity and movement of trawler-associated dolphins in the Pilbara Trawl Fishery

The dedicated photo-identification effort of 12, 20 min samples immediately before winch-up from one trawler over two fishing trips, spanning some 60 trawls over two weeks, identified less than 150 individual dolphins. More than a third of these dolphins (50) were photographed three to seven times and estimates of the number of dolphins associating with one of the three trawlers in the fleet varied between 170 and 280, depending on the type of model used. This represents just 7-12% of the total abundance of dolphins across the entire area of the PTF, as estimated by the simultaneous aerial survey. These data suggest that at least a proportion of the population show fidelity to trawler-associated foraging over days and weeks. These results parallel those of Jaiteh et al. (2013), who found that individual dolphins were resighted on video footage collected inside a trawl net during different days and between separate fishing trips in the PTF over days and weeks.

Three distinctive individuals in the catalogue constructed from the dedicated photo-identification work were matched with opportunistically collected photographs taken from the stern of trawlers in 2008, and five individuals were genetically matched with samples collected in 2008. Each genetic re-sampling event occurred within 140 km of the initial sampling event, regardless of the time between the events. One individual was sampled just 15 km from where it was originally sampled in 2008. It can be inferred from these data

that at least some individuals also show fidelity to foraging behind trawlers over months to years. Resident communities of bottlenose dolphins (both *T. truncatus* and *T. aduncus*) are well known for developing foraging 'traditions' over years and even between multiple generations (e.g., Krützen et al. 2005; Sargeant et al. 2005; Daura-Jorge et al. 2012) and trawler-associated foraging by dolphins has now been reported in numerous locations around the world (e.g., Chilvers and Corkeron 2001; Kovacs and Cox 2014).

Many coastal bottlenose dolphin populations (again, both *Tursiops* spp.) consist largely of 'residents' to a particular area (Shane et al. 1986; Connor et al. 2000), although movements in the order of hundreds to over a thousand km have been reported for some individuals (e.g., Greece - Bearzi et al. 2011; United Kingdom – Robinson et al. 2012; southern California and north-western Mexico – Hwang et al. 2014). Far less is known of pelagic populations. Again, a few individuals have been documented moving considerable distances in short periods, i.e. thousands of kilometres (Wells et al. 1999), but some offshore populations appear to include individuals with discrete home ranges and that display long-term site fidelity (e.g., Rossbach and Herzing 1999). Results from this study suggest movements in the order of tens to hundreds of kilometres only and a strong degree of fidelity to trawler-associated foraging for a proportion of the PTF-associated population.

4.3.3 Conclusions and recommendations

The abundance and density of bottlenose dolphins interacting with the PTF off north-western Australia is considerably lower than in comparable regions in the Gulf of Mexico, and similar in magnitude to some heavily degraded areas in the Mediterranean Sea. There are a number of plausible reasons for this, including being unable to account for availability bias in this study resulting in an under-estimate of abundance, possible marked

differences in productivity between regions, or that historical and ongoing dolphin bycatch has impacted dolphin abundance. The population, or at least the portion of the population that interacts with the PTF, is subject to bycatch levels in trawl nets similar in magnitude to those in the western North Atlantic off the USA's east coast, where the minimum population estimate of *T. truncatus* over a large area exceeds 55,000 offshore individuals (Waring et al. 2014). The combined elements of this study show that the number of dolphins interacting with the Pilbara Trawl Fishery is smaller than previously believed, and that a proportion of this community displays a high degree of fidelity to trawler-associated foraging over days to years. These findings lead to the following recommendations:

i. A prescriptive limit should be placed on the number of human caused mortalities in the dolphin population. This limit should be established according to internationally accepted standards (e.g., Wade 1998; Thompson et al. 2000);
ii. An independent observer program is again required in the PTF, at coverage levels of 30-62%, in order to objectively estimate total bycatch with greater precision than has been achieved with self-reporting (Read 2010; Allen et al. 2014);
iii. Further estimates of abundance over a wider area are required in order to establish trends in dolphin population size and rigourously assess risks of ongoing human impacts. The use of unmanned aerial vehicles for this purpose may be more accurate, free of risk to humans and less costly than manned aerial surveys (Hodgson et al. 2013). Furthermore, data on the surfacing intervals and dive times of common bottlenose dolphins in and around the PTF are required in order to explicitly correct for availability bias in future abundance estimates;
iv. This information should be used in combination with data on the biology of bottlenose dolphins (generation time, reproductive output) to conduct a Population

Viability Analysis (Shaffer 1990; Thompson et al. 2000) before further assumptions are made regarding the population's conservation status;

v. Successive State and Commonwealth governments have determined "acceptable" dolphin bycatch limits and granted accreditation to the PTF in the absence of fundamental data on mortality rates and dolphin population size. The results of the current research should be used to better-inform future management of the PTF and its impacts on populations of endangered, threatened and protected species.

Appendix 4.1: ***Aerial survey: Model details and selection results for the mark-recapture distance sampling (MRDS)***

Table 4.7. MRDS analysis of bottlenose dolphin dual observer data. The best FI model (selected based on AIC scores) is shown in bold. Covariate terms are as follows: Dist = distance, B = Beaufort sea state, CA = calf presence, CC = cloud cover, F = fatigue, G = glare intensity, GA = glare angle, S = group size, T = Time of day. Colons ":" code for variable interactions. Derived parameters include animal density (D), abundance (N) and associated 95% CI (N_{low}; N_{high}).

	Model	**Point Independence**							**Full Independence**					
		g. (y, z)	**N**	**N_{low}**	**N_{high}**	**D**	**AIC**	**ΔAIC**	**ΔAIC**	**N**	**N_{low}**	**N_{high}**	**D**	**AIC**
1	Dist	1	1,823	1,090	3,049	0.09988	192.6	82.4	6.4	1,321	757	2,306	0.07237	116.6
2	Dist	CC	2,104	1,170	3,785	0.11528	192.9	82.7	-	-	-	-	-	-
3	Dist	GA	1,897	1,086	3,313	0.10395	194.8	84.6	-	-	-	-	-	-
4	Dist	S	1,646	1,000	2,709	0.09019	192.5	82.3	-	-	-	-	-	-
5	Dist	T	1,817	1,085	3,045	0.09957	194.5	84.3	-	-	-	-	-	-
6	Dist	S+G	1,686	908	3,131	0.09236	196.9	86.7	-	-	-	-	-	-
7	Dist	S+T	1,643	992	2,719	0.09000	194.4	84.3	-	-	-	-	-	-
8	Dist	S+B	1,691	1,017	2,814	0.09267	194.2	84.1	-	-	-	-	-	-
9	Dist+B	S	1,648	1,001	2,714	0.09029	194.3	84.1	8.6	1,320	754	2,311	0.07231	118.8
10	Dist+CA	S	1,655	1,004	2,728	0.09069	192.0	81.8	6.7	1,331	759	2,334	0.07291	116.9
11	Dist+CC	S	1,647	1,001	2,709	0.09021	193.5	83.3	8.8	1,581	742	3,367	0.08662	119.0
12	Dist+F	S	1,650	1,002	2,718	0.09041	193.4	83.2	6.1	1,370	768	2,443	0.07506	116.3
13	Dist+G	S	1,677	1,011	2,781	0.09188	194.0	83.8	4.2	1,526	797	2,922	0.08362	114.4
14	Dist+GA	S	1,652	1,001	2,726	0.09049	193.4	83.2	6.5	1,357	755	2,439	0.07436	116.7
15	Dist+S	S	1,643	999	2,703	0.09001	194.4	84.2	7.7	1,314	756	2,284	0.07199	117.9
16	Dist+T	S	1,647	1,002	2,706	0.09023	193.2	83.0	4.4	1,369	780	2,401	0.07500	114.6

17	Dist+T+B	S	1,648	1,003	2,709	0.09028	195.2	85.0	6.7	1,366	777	2,401	0.07484	116.9
18	Dist+T+CA	S	1,654	1,006	2,721	0.09064	193.2	83.0	5.7	1,366	777	2,401	0.07484	115.9
19	Dist+T+F	S	1,653	1,006	2,716	0.09055	193.2	83.0	1.2	1,484	814	2,705	0.08129	111.4
20	Dist+T+G	S	1,680	1,017	2,776	0.09205	195.0	84.8	2.9	1,578	818	3,046	0.08647	113.1
21	Dist+T+GA	S	1,651	1,003	2,716	0.09043	193.5	83.3	2.7	1,430	790	2,587	0.07835	112.9
22	Dist+T+S	S	1,646	1,002	2,705	0.09018	195.2	85.0	6.2	1,367	779	2,399	0.07487	116.4
23	Dist+B+G	S	1,684	1,013	2,799	0.09228	195.8	85.6	6.6	1,532	791	2,967	0.08393	116.8
24	Dist+S+G	S	1,669	1,010	2,759	0.09143	195.9	85.7	5.3	1,491	792	2,809	0.08170	115.5
25	Dist+G+F	S	1,679	1,011	2,788	0.09197	195.8	85.6	5.4	1,554	799	3,022	0.08514	115.6
26	Dist+S+B	S	1,645	999	2,707	0.09010	196.2	86.0	9.8	1,313	753	2,288	0.07191	120.0
27	Dist+S+F	S	1,646	1,000	2,707	0.09016	195.3	85.1	7.1	1,356	767	2,398	0.07429	117.3
28	Dist+S+GA	S	1,649	1,000	2,721	0.09036	195.4	85.2	8.1	1,349	751	2,424	0.07390	118.3
29	Dist+T+F+S	S	1,650	1,004	2,711	0.09040	195.2	85.0	2.7	1,473	810	2,679	0.08072	112.9
30	**Dist+T+F+GA**	S	1,656	1,006	2,728	0.09075	193.7	83.5	**0.0**	**1,551**	**822**	**2,929**	**0.08499**	**110.2**
31	Dist T+F+G	S	1,679	1,016	2,776	0.09201	196.3	86.1	2.8	1,633	833	3,203	0.08948	113.0
32	Dist+T+F+CA	S	1,659	1,009	2,729	0.09089	193.6	83.4	3.3	1,463	804	2,660	0.08013	113.5
33	Dist T+F+GA+F:T	S	1,657	1,005	2,733	0.09079	195.7	85.5	2.1	1,551	821	2,930	0.08497	112.3
34	Dist+T+F+GA+F:GA	S	1,699	981	2,945	0.09311	194.7	84.5	3.2	1,609	680	3,805	0.08814	113.4
35	Dist+T+F+GA+F:GA+F:T	S	1,709	981	2,978	0.09363	196.6	86.4	6.3	1,604	676	3,803	0.08786	116.5
36	Dist+T+F+S+S:F	S	1,762	972	3,193	0.09654	193.6	83.4	3.0	1,855	646	5,325	0.10163	113.2
37	Dist+T+F+B+F:B	S	1,651	1,004	2,712	0.09043	196.7	86.5	3.2	1,520	827	2,793	0.08325	113.4
38	Dist T+F+GA+S+S:F	S	1,768	964	3,243	0.09687	194.3	84.1	2.3	1,989	640	6,182	0.10899	112.5

Chapter Five: Conclusions and recommendations

5.0 Conclusions

In my Thesis, I have provided the first rigorous evaluation of the interactions between dolphins and a demersal trawl fishery off remote north-western Australia. This has been achieved through research into three major components of the interactions: a detailed analysis on the extent of dolphin bycatch and its spatial and temporal variation (Chapter 2); establishing the identity of the dolphin species and the fishery-impacted community's degree of connectivity with adjacent, coastal populations (Chapter 3); and, estimating the abundance and degree of fidelity of the dolphins interacting with the fishery (Chapter 4).

The comprehensive analysis of skippers' logbook and independent observer data showed that an estimated minimum of 500 dolphins were caught in the Pilbara Trawl Fishery in the ten years from 2003-2012 (Chapter 2; Allen et al. 2014). Dolphin bycatch numbers from the 1970s and 1980s, when foreign trawling fleets fished the North West Shelf with far greater fishing effort than the last two decades of fishing by the Australian fishery (Althaus et al. 2006; Department of Fisheries 2013), are unknown, but are likely to have been much higher than the current bycatch levels. The number of dolphin captures being reported by skippers decreased after the compulsory introduction of Bycatch Reduction Devices in 2006 from above 50 to between 17 and 23 individuals per annum (Department of Fisheries 2013; Chapter 2). The most recent skippers' logbook data, however, indicated an increase in dolphin bycatch rates above the levels reported after 2006 (Department of Fisheries 2013). There has been no ongoing independent observer coverage in the PTF since late 2009,

so estimates of dolphin bycatch for subsequent years are uncertain. Nevertheless, six-months of data from an electronic (video) observer system are available for the 2012 calendar year (Wakefield et al. 2014). Skippers reported 29 dolphin captures in just over 10,000 h of trawling (or a rate of 2.9 dolphins/1,000 h), 24 of which were confirmed dead (2.4 dolphins/1,000 h) (Department of Fisheries 2013). The electronic observer system monitoring bycatch in 2012 documented seven dolphin captures in just over 1,000 h of trawling (or 7.0 dolphins/1,000 h), five of which were confirmed dead (5.0 dolphins/1,000 h) (Wakefield et al. 2014). Based on the total hours trawled in the fishery in 2012 (10,269 h, Department of Fisheries 2013), the level of bycatch documented with the electronic observer system (Wakefield et al. 2014) is equivalent to the bycatch of about 50-70 dolphins per annum.

The level of dolphin bycatch and the discrepancy between numbers reported by skippers and the electronic observer system in Wakefield et al. (2014) are very similar in magnitude to the data reported in Chapter 2, in which independent observers reported just over double the bycatch rate reported by skippers (about 50 individuals per annum, Chapter 2; Allen et al. 2014). This highlights the importance of collecting independent data to determine total bycatch. Both the initial and recent assessments of the threat posed by bycatch to the dolphin population, i.e., that the rate of fisheries-related mortalities through bycatch poses "negligible risk" to the dolphin population (Department of Fisheries 2004b; Wakefield et al. 2014), do not acknowledge under-reporting in skippers' logbooks or unaccounted dolphin bycatch. These assessments were also made in the absence of fundamental data on the dolphin population (Chapters 3 and 4) and require revision in light of the research presented in this Thesis.

The research in Chapter 3 of this Thesis clearly identified that the dolphins impacted by the Pilbara Trawl Fishery are common bottlenose dolphins (*Tursiops truncatus*) that are genetically isolated from the adjacent, coastal Indo-Pacific bottlenose dolphins (*T. aduncus*) populations. The fishery-associated *T. truncatus* are also differentiated from the *T. truncatus* sampled 300 km to the south-west. However, a greater number of *T. truncatus* samples is needed from outside (east, west and north) of the fishery before conclusions can be drawn on whether the dolphins associating with the PTF are an isolated unit or form part of a broader, larger, pelagic *T. truncatus* population (Chapter 3).

Nearly 20 years ago, *T. truncatus* were listed as "no category assigned because of insufficient information" in the Action Plan for Australian Cetaceans (Bannister et al. 1996) and little has changed since then. They have more recently been assigned the category "data deficient" in the Action Plan for Australian Mammals (Woinarski et al. 2014). Due to this lack of knowledge, assessing the conservation status of the majority of *T. truncatus* populations is not yet possible. The abundance of *T. truncatus* across the ca. 23,000-km^2 area of the PTF was estimated in Chapter 4 at ca. 2,000-3,000 individuals. While this estimate is fewer than expected, the lack of correction factors to account for availability bias in Australian dolphins mean it is likely to be an under-estimate. The population as a whole being larger than this is, however, probably mediated by the fact that there is a community of dolphins within the broader population that show long-term fidelity to foraging around trawlers (Chapter 4).

An objective of the *Guidelines for the Ecologically Sustainable Management of Fisheries* (2007) and provisions of the EPBC Act (1999) stipulate that a commercial fishery should receive accreditation to operate and export product only if its management regime, policies and plans ensure that:

(*i*) The individuals or entities engaged in fishing take all reasonable steps to ensure that endangered, threatened and protected (ETP) species are not killed or injured as a result of the fishing;

(*ii*) There is an assessment of the impact of the death or injury of ETP species in the fishery on their conservation status to ensure that species, or populations of those species, are not adversely affected; and

(*iii*) The management response, considering uncertainties in the assessment and precautionary management actions, has a high chance of achieving the objective and that administrative decisions consider the precautionary principle.

The way in which the "acceptable" annual limit of dolphin bycatch was originally calculated ("The catch limit of 75 individuals is derived from the bycatch survey catch [ca. 50 per annum] plus 50% to allow for a possible underestimation", Department of Fisheries 2004a) and the interpretation of the data presented in Wakefield et al. (2014) demonstrate that these objectives and provisions have not yet been met for the PTF. The gaps in our understanding of small cetacean populations, especially across north-western Australia, and the extent of their interactions with the PTF framed the objectives of this thesis. I have estimated total dolphin bycatch; assessed the species identity and degree of connectivity of dolphins interacting with the PTF with adjacent populations; and, estimated the abundance and fidelity of dolphins interacting with the PTF.

5.1 Recommendations

Based on the results of my research on the levels of bycatch in the fishery, the dolphin species identity and connectivity with adjacent, related populations of dolphins and the first estimates of abundance for *T. truncatus* in the managed areas of the Pilbara Trawl Fishery, I make the following recommendations for reducing dolphin bycatch and improving monitoring and mitigation:

(1) Overall trawling effort should be reduced in the PTF to reduce dolphin bycatch below a prescriptive limit that is established according to internationally accepted standards;

(2) Trawl nets should include Bycatch Reduction Devices with both top- and bottom-opening escape hatches in order to facilitate the escape of air-breathing and other megafauna, as well as the expulsion of large benthos;

(3) Independent (human) observer coverage and in-net video collection should resume in order to quantify ongoing bycatch with greater precision and power;

(4) Biopsy samples should be collected from adjacent *T. truncatus* populations to better-assess population boundaries, gene flow and the impact of historical and on-going bycatch;

(5) Further abundance estimates, based on repeated surveys over the entire area of the PTF, are required as soon as possible, in order to establish any trends in dolphin abundance. Precautionary management action should not, however, be delayed until a decline in abundance is detected (Thompson et al. 2000);

(6) Independent data on the surfacing intervals and dive times of *T. truncatus* in and around the PTF should be collected in order to quantify availability bias on the transect line. Suitable correction factors should then be applied to improve the level of certainty around future abundance estimates;

(7) Already available data should be used in combination with data on the biology of *T. truncatus* in order to inform a Population Viability Analysis – a process involving the evaluation of population data and models to anticipate the likelihood that the population will persist for an arbitrarily determined time into the future under a number of threat scenarios (Shaffer 1990; Boyce 1992);

(8) In accordance with the provisions of the EPBC Act and the objective of the *Guidelines for the Ecologically Sustainable Management of Fisheries,* determinations by both State and Commonwealth resource management agencies on the level of impact that bycatch has on protected populations in the Pilbara Trawl Fishery should be reviewed to take into account the results from this Thesis.

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Appendix 1: Peer-reviewed publications during candidature

14. Brown A, Kopps AM, **Allen SJ**, Bejder L, Littleford-Colquhoun B, Parra GJ, Cagnazzi D, Thiele D, Palmer C and Frere C 2014. Population differentiation and hybridisation of Australian snubfin (*Orcaella heinsohni*) and Indo-Pacific humpback dolphins (*Sousa chinensis*) in north-western Australia. PLoS ONE 9: e101427

13. Jaiteh VF, **Allen SJ**, Meeuwig JJ and Loneragan NR 2014. Combining in-trawl video with observer coverage improves understanding of protected and vulnerable species bycatch in trawl fisheries. Mar Freshw Res 65: 1-8

12. Krützen M, Kreicker S, MacLeod CD, Learmonth J, Kopps AM, Walsham P and **Allen SJ** 2014. Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (*Tursiops* sp.) provides access to a novel foraging niche. P Roy Soc Lond B Bio 281: 20140374

11. Allen SJ, Tyne J, Kobryn HT, Bejder L, Pollock KH and Loneragan NR. 2014. Patterns of dolphin bycatch in a North-Western Australian trawl fishery. PLoS ONE 9: e93178

10. Allen SJ 2014. From exploitation to adoration: The historical and contemporary contexts of human-cetacean interactions. In Whale-Watching: Sustainable Tourism and Ecological Management (Higham J, Bejder L, Williams R eds). Pp. 31-47. Cambridge Uni Press.

9. Kopps AM, Ackermann C, Sherwin WB, **Allen SJ**, Bejder L and Krützen M 2014. Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. P Roy Soc Lond B Bio 281:20133245

8. Kopps AM, Krützen M, **Allen SJ**, Bacher K and Sherwin W. 2013. Characterizing the socially transmitted foraging tactic "sponging" by bottlenose dolphins in the western gulf of Shark Bay, Western Australia. Mar Mamm Sci 30: 847-863

7. Jaiteh VF, **Allen SJ**, Meeuwig JJ and Loneragan NR 2013. Subsurface behaviour of bottlenose dolphins (*Tursiops truncatus*) interacting with fish trawl nets in north-western Australia. Mar Mamm Sci 29: E266-E281

6. Brown A, Bejder L, Cagnazzi D, Parra G and **Allen S** 2012. The North West Cape, Western Australia: A potential hotspot for Indo-Pacific Humpback Dolphins *Sousa chinensis*? Pac Conserv Biol 18: 240-246

5. Nicholson K, Bejder L, **Allen SJ**, Krützen M and Pollock KH 2012. Abundance, survival and temporary emigration of bottlenose dolphins (*Tursiops* sp.) off Useless Loop in the western gulf of Shark Bay, Western Australia. Mar Freshw Res 63: 1059-1068

4. Allen SJ, Cagnazzi DD, Hodgson AJ, Loneragan NR and Bejder L 2012. Tropical inshore dolphins of north-western Australia: Unknown populations in a rapidly changing region. Pac Conserv Biol 18: 56-63

3. Bejder L, Hodgson A, Loneragan N and **Allen S** 2012. Coastal dolphins in north-western Australia: The need for re-evaluation of species listings and short-comings in the Environmental Impact Assessment process. Pac Conserv Biol 18: 22–25

2. Tyne JA, Loneragan, NR, Kopps AM, **Allen SJ**, Krützen M and Bejder L 2012. Ecological characteristics contribute to sponge distribution and tool use in bottlenose dolphins *Tursiops* sp. Mar Ecol Prog Ser 444: 143–153

1. Allen SJ, Bejder L and Krützen M 2011. Why do Indo-Pacific bottlenose dolphins (*Tursiops* sp.) carry conch shells (*Turbinella* sp.) in Shark Bay, Western Australia? Mar Mamm Sci 27: 449–454